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HUMAN PHYSIOLOGY

HUMAN PHYSIOLOGY

ELEMENTS
OF
HUMAN PHYSIOLOGY

BY
L. HERMANN

PROFESSOR OF PHYSIOLOGY IN THE UNIVERSITY OF ZÜRICH

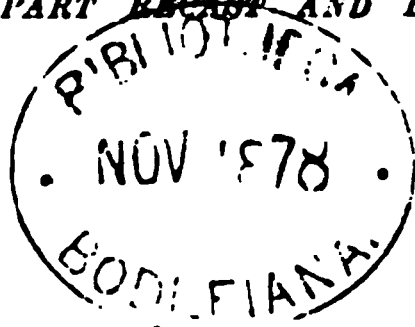
TRANSLATED AND EDITED FROM THE SIXTH EDITION

BY
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SECOND EDITION

IN GREAT PART RECAST AND ENLARGED



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165. e. 59.

PREFACE

TO

THE SECOND EDITION.

THE PRESENT EDITION differs from the first in the following particulars:—

Firstly. The German text having been very materially altered, and in some parts entirely recast, many sections of the work have had to be retranslated from the last (sixth) edition. Through the kindness of Professor Hermann, the proof sheets of the latter were forwarded to me before publication.

Secondly. Wherever it appeared to me likely to conduce to the interests of the English reader, I have supplemented the text by the addition of new matter. By adopting a different type, the publishers have succeeded in compressing within the same space about one-sixth more matter than was contained in the first edition. Except in the sections which treat of the chemical constituents of the animal body (pp. 12–58), and which precede chap. i., I have taken care to distinguish the added or interpolated matter by enclosing it in brackets, thus []. In those sections, however, the alterations and additions were so numerous as to render this plan impracticable, and accordingly it is impossible for the reader to distinguish where I have added to or modified the text. The reader will therefore hold Professor Hermann entirely irresponsible for any views or statements introduced into the text from pages 12–58 inclusive.

Many readers had remarked upon the brevity with which the functions of the cranial nerve were treated of in Professor

Hermann's work, and I have in the present edition added very greatly to the information contained in the German text. A summary of the anatomical distribution of each nerve has been added, illustrated by admirable diagrams, for which I have to thank my friend Dr. Alfred Young, Assistant Lecturer on Anatomy in Owens College.

Thirdly. Where it appeared to me to be necessary, diagrams or drawings of apparatus used in physiological research and description of experimental methods have been introduced; for most of these drawings also I am indebted to Dr. Young.

Fourthly. I have supplied references to the most important memoirs by the writers referred to in the text.

In conclusion, I have to express my thanks to Mr. Priestley for help afforded to me in drawing up the Index of the present edition, and to several correspondents who most courteously drew my attention to errors which they had discovered in the first edition; especially I wish to express my acknowledgments to Mr. Alfred Benson, of St. Mary's Hospital.

ARTHUR GAMGEE.

OWENS COLLEGE:

September 1878.

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ERRATA.

- Page 36, bottom line, ~~for~~ $\text{CO}(\text{NH}_2)_2$, *read* $\text{CO}(\text{NH}_2)_2$.
,, 39, line 22, *for* Glycococine *read* Glycocine.
,, 61, ,, 19, *for* Ocooid *read* Oecoid.
,, 101, ,, 9, ~~for~~ expiration *read* inspiration.
,, ,, 10, *for* inspiratory *read* expiratory.
,, 137, ,, 28, *delete up*.
,, 147, ,, 24, *for* glycine *read* glycocine.
,, 148, ,, 28, *for* glycine *read* glycocine.
,, 360, ,, 36, *insert* 34.
,, 463, ,, 15, *for* deafens *read* deadens.
,, 530, ,, 7, *delete* the inverted comma

INTRODUCTION.

PHYSIOLOGY is the science which treats of the normal processes which have their seat in the living bodies or organisms of plants and animals. The processes which are characteristic of living beings, and whose sum constitutes life, may be classified as orderly changes of (1) their chemical constituents; (2) the forces which work within them; and (3) their form. Formerly an attempt was made to explain the peculiar processes which have their seat in the animal organism, by supposing it to be endowed with properties special to it, and heritable, depending on a supposed '*vital force*.' This vague conception has, however, been abandoned since the laws of inorganic nature have been discovered to preside over the most thoroughly investigated processes of life, and especially since the application to the organic world of a great principle of modern science has taught us the relations which exist between the changes in the matter and the forces of organised beings. Relying upon this knowledge, we believe that the forces of living are the same as those of inanimate bodies, and that they obey the same laws; and, consequently, that it will ultimately be possible to explain the hitherto incomprehensible phenomena of living beings, particularly their morphological processes, by physical and chemical laws. This conception possesses, quite apart from its probability, the great merit of introducing into the study of organic nature more precise views and more accurate research, and, although it has not been rigidly proved, will, in the present work, tacitly underlie the exposition of the processes of the human organism.

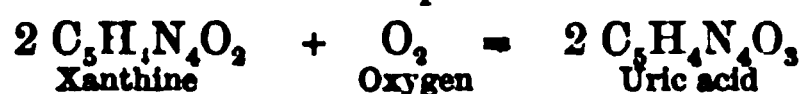
The human body, like that of every other animal, is an organism in which, by the chemical changes of its constituent parts, *potential* is converted into *kinetic* energy.

These chemical changes depend on the presence, within the organism, of energy-yielding substances.

The greater number of the chemical operations which occur in the living body, and which are accompanied with the manifestation of kinetic energy, are oxidations, or decompositions which depend on oxidation; nevertheless, there are, in all probability, other pro

cesses which are so accompanied. The energy-yielding material of the organism is chiefly represented, on the one hand, by oxidizable (organic) combinations; on the other by free oxygen.

The following is an instance of a simple oxidation:

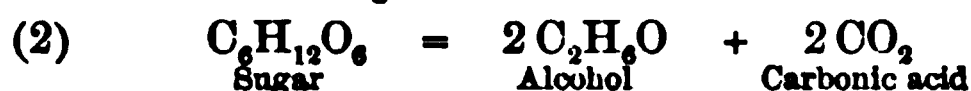
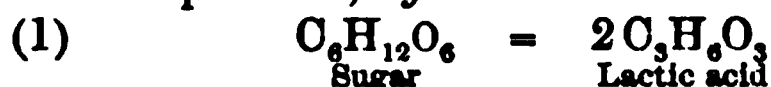


An example of a decomposition depending on oxidation is:

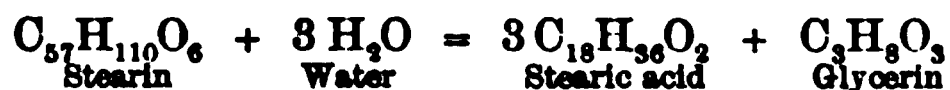


The following may be adduced as examples of other decompositions occurring in the body, and which are associated with a manifestation of kinetic energy:

a. Simple decompositions, *e.g.*



b. Hydrolytic decompositions, in which a body splits up after combining with the elements of water:



Every act of the organism must diminish, to a corresponding extent, the energy-yielding store which it contains. As the products of the chemical changes, even when they, in the first place, have definite purposes to fulfil in the body, are ultimately thrown off from it; and, moreover, as the reconversion of these products into the substances from which they were originally derived would require the expenditure of as much energy as is generated during the process of decomposition, it follows that a restitution of energy-yielding substances can only take place from without. It is, therefore, essential, in order that the organism should continue to exist, that it be continuously supplied with free oxygen and oxidizable substances. The latter are called *the organic constituents of food*.

In addition to its energy-yielding constituents, the organism possesses other (inorganic) substances, which do not furnish it with energy. Their uses are only imperfectly ascertained, though they appear, in great part, to be mechanical. Some serve as solvents for organic bodies, some play an important part in the formation of the solid parts of the body, whilst others are in complex combination with essential organic constituents. Even the inorganic substances are continually being thrown out of the body in certain quantities, serving, in part, as solvents for the products of decomposition which have to be eliminated. The inorganic substances of the body, therefore, like the organic, have to be continually replaced by others taken from without, which constitute *the inorganic constituents of food*.

It follows from what has been said that the existence of the organism is associated with a continual movement of matter into

and out of it, which constitutes what may be termed the *exchange of material* of the organism (Stoffwechsel des Organismus).

The plant takes the products of the chemical operations of the animal body (carbonic acid, water, ammoniacal salts) and reduces them; it arranges their radicals (carbon, hydrogen, nitrogen, &c.) side by side, combines them with oxygen, and, storing them up within itself as organic compounds, it restores the greater part of the liberated oxygen to the atmosphere. In the separation of the once combined molecules, a certain amount of kinetic energy is expended, which is exactly equal to the amount of potential energy remaining in the separated elements: we may, therefore, say that in the process of reduction kinetic is converted into potential energy. The kinetic energy which the plant receives is apparently yielded to it, first by conducted heat (plants cool the bodies in their vicinity), secondly by radiated heat, thirdly by absorbed light (chemical rays). The potential energy into which these forms of kinetic energy are converted is associated with the liberated oxygen and the oxidizable organic compounds stored up in the plant. (We must not forget, however, that even in plants there occur processes which are similar in nature to those which are characteristic of the animal body; thus many of the parts of plants generate heat. Further, the processes of development in the plant, as in the animal, require kinetic energy.) From what has been stated there follows the most weighty conclusion, viz. that the vegetable and animal kingdoms are mutually dependent on one another. The plant, acting as a reducing agent, converts kinetic into potential energy; the animal, acting as an oxidizing agent, converts potential into kinetic energy. The plant uses the oxidation-products of the animal, CO_2 , H_2O , &c.; the animal uses the reduction-products of the plant— O , on the one hand, and the organic compounds of C, H, N, O, &c., on the other. These organic compounds built up by the plant, if we except inorganic matters, constitute the only nourishment of animals, for even carnivorous animals merely consume the elements of vegetable food which have been modified and stored up for a time in the tissues of the creatures upon which they feed.

The amount of kinetic energy developed in the chemical processes of the organism is entirely determined (in any case) by the nature of the process and the amount of the constituents which take part in it. The *modes of motion*, however, in which the kinetic energy manifests itself, the *activities* of the body, which result from the chemical changes, depend upon conditions with which we are unacquainted. We merely know that certain results are associated with specific apparatuses of the body, which we term *organs*, and which are distinguished from one another, not only by the substances which they contain (their chemical composition), but also by their peculiar structure. The most general forms of motion which result from chemical changes are heat, and changes in the state of aggregation and in form. These changes may either proceed with imperceptible slowness in the smallest parts, and are then designated *growth*, *division*, &c., or they manifest themselves on a larger scale as the visible motion of masses (*mechanical work*). Electricity is also one of the forms of energy which result from chemical changes; in many animals there is also an evolution of light.

The same organ can, either simultaneously or at different times, give rise to different manifestations of energy.

There exist well-known (equivalent) quantitative relations between the various forms of motion. A decomposition which, if leading to the formation of heat, develops one heat-unit, will, if it accomplishes mechanical work, perform 424 grammetres of work; ¹ one unit of heat can therefore be converted into 424 grammetres of work, and conversely.

The chemical changes, and consequently the activities of the body, are in great part, if not altogether, subjected to a certain regulating influence, which proceeds from a peculiar apparatus which we denominate the *nervous system*. This influence, naturally, affects not only the amount and nature of the products of chemical change, but also the amount of energy which becomes kinetic, *i.e.* it affects the acts performed by the body. According to our views of the functions of an organ do we place this or that effect of the influence in the foreground. Thus in the case of a muscle we regard the influence of a nerve on its motion, and therefore on the work which it can accomplish, as the essential effect; whilst we habitually overlook the simultaneous influence which the nerve exerts on the quantity of the chemical products which are generated in the muscle. In glands, on the contrary, the influence which the nerves supplying them exert on their chemical products, *viz.* on the specific constituents of their secretions, appears to be the essential result, whilst the contemporaneous influence on the production of heat, *i.e.* on the evolution of kinetic energy, is usually neglected.

The mode in which this influence of the nervous system is exerted is as yet quite unknown to us. From a mechanical point of view, this influence may be regarded as a *liberating force*, *i.e.* as a force which leads to a conversion of a certain amount of potential into kinetic energy.

It is well known that an infinitely small liberating force may liberate large quantities of kinetic energy, and it is exceedingly probable that even the liberating forces of the nervous system, if measured as forces, would be very small in amount, and consequently that the chemical changes necessary to their evolution, as to that of all the other forces of the organism, are but of small magnitude.

A second equally obscure influence of the nervous system is that which conditions the bodily acts by which the liberated energy manifests itself; this qualitative influence of the nervous system appears to be closely associated with its influence on the quantity of the energy transformed.

The following remarks may render more easy the conception of a 'liberating force.' A liberating force is one which removes any hindrance or impediment to the conversion of potential into kinetic energy. A clock wound up, but prevented from going by a catch, represents a certain amount of potential

¹ A unit of heat is the amount of heat which is required to raise the temperature of 1 gramme of water 1° Centigrade. A grammetre is the amount of work expended in lifting 1 gramme to the height of 1 metre.

energy; the position of its weights or of its spring cannot then be converted into motion. So soon, however, as the catch is withdrawn, the potential energy becomes kinetic, the weight falls or the spring approaches its original form, and the clock goes. The force which removes the catch, which therefore liberates the clock, and liberates its potential energy, may be called 'the liberating force.' Its magnitude often bears no proportion to that of the energy set free; the same force which withdraws the catch which impeded the motion of a clock driven by a gramme weight, might also liberate a clock driven by a hundred weight.

Other examples of such liberations are:—

A spark which inflames a mass of gunpowder, and consequently sets free enormous quantities of energy, or a slight movement which closes the circuit of a powerful battery. There occur, however, cases of liberation in which the liberating force does not, as in the cases cited above, instantly set free the whole store of energy, but only a portion, which bears a definite, though it may be a complicated, relation to its own magnitude. Let us take the case of a head of water confined by a sluice with a rectangular door. The quantity of water which will flow out, and the kinetic energy represented by its fall, will depend upon the height to which the sluice-door has been raised, and upon the force—here acting as a liberating force—expended in raising it.

All the phenomena of liberation which occur in the body appear to bear some resemblance to the last case which has been cited.

A closer survey of the nervous system reveals the fact that not only does it exert a liberating influence on the *organs of work* of the body, but that its own constituent parts exert a similar action one upon the other. By organs of work we may shortly designate those organs, such as muscles and glands, in which considerable amounts of energy become kinetic and apparent to us in the form of mechanical work, heat, &c.

A portion of the nervous system—that engaged in conducting—may be looked upon as consisting of series of elementary parts, of which each one possesses a certain amount of potential energy, and which are so closely connected together that the energy which has been liberated in one part serves to liberate the energy of the adjoining elementary parts; thus, a liberating force which acts on the first of these elementary parts produces a series of liberations, until at last the energy set free in the ultimate particles situated in some other organ (as an organ of work) brings about the liberation of forces within that organ. We distinguish two kinds of *liberating-chains*, possessing distinct origins and termination. The one kind proceeds from the so-called organs of the senses, *i.e.* from organs on which an external influence (as pressure, heat, sound, light, &c.) acts as a liberating agent, and terminates in the so-called *central organs of the nervous system*; to which we give the name of centripetal chains, or centripetal nerves. The second kind (the centrifugal chains), on the other hand, proceeds from the central organs of the nervous system, and terminates in the organs of work.

The central organs of the nervous system may, consequently, be looked upon as the points of departure and of entrance of liberating-chains. We are, however, unacquainted with the nature

INTRODUCTION.

processes which, in the case of centrifugal chains, act as causes, or in the case of centripetal chains are the result of influences which travel to the centre. In reference to these, we merely possess hypotheses which will be discussed in a chapter which treats of the central organs of the nervous system.

Here, it may however be merely mentioned, that there are many cases in which the question appears to be easily solved, as in which a centripetal chain, acting through a central organ, immediately liberates a centrifugal chain, so that essentially there exists only a single chain commencing in a sense-organ and terminating in a work-organ (reflex action).

Finally, we must mention that in a part of the central organs there are material processes—amongst others such as are capable of generating centrifugal chains and such as are the results of centripetal influences—are accompanied, in an inexplicable manner, by wholly undefinable phenomena, which characterize the *states of consciousness*. The term *mind* may be applied to the complex of all the actual and possible states of consciousness of the organism.

It is not the province of Physiology to investigate the molecular details of the organism, and to connect with these all its functions. The means of treating in a scientific manner the phenomena of 'mind' are completely wanting, inasmuch as these phenomena cannot be brought into relation with any of our scientific conceptions. Physiology must here, therefore, provisionally restrict itself to the investigation of the organs with which they are connected. Even of the remaining tasks of the science, the number of which we may venture to designate as possible, but a small part has been really accomplished.

It is difficult to follow a strictly logical course in the exposition of facts which have been already discovered. Seeing that our knowledge of the relation between the chemical processes and the organism is so limited that it is nearly all included in the general observations which have already been made, it is in vain to attempt to expound them in their natural and actual relations. It is more convenient, therefore, to connect two distinct parts of this work the *Material exchanges* and the *Transformations of Energy* of the organism. But here a difficulty arises out of the mutual relations of the organic processes. The forces of the organism are often employed in their own matter, so that a knowledge of these forces is required in the first place, for the proper understanding of the material processes. Hence it happens that even in the First Part of this

of the processes which, in the case of centrifugal chains, act as liberating causes, or in the case of centripetal chains are the result of the influences which travel to the centre. In reference to these questions, we merely possess hypotheses which will be discussed in the section which treats of the central organs of the nervous system. Here, it may however be merely mentioned, that there are many cases in which the question appears to be easily solved, viz. cases in which a centripetal chain, acting through a central organ, immediately liberates a centrifugal chain, so that essentially there exists only a single chain commencing in a sense-organ and terminating in a work-organ (reflex action).

Finally, we must mention that in a part of the central organs certain material processes—amongst others such as are capable of liberating centrifugal chains and such as are the results of centripetal liberations—are accompanied, in an inexplicable manner, with wholly undefinable phenomena, which characterize the *states of consciousness*. The term *mind* may be applied to the combination of all the actual and possible states of consciousness of the organism.

It is the province of Physiology to investigate the molecular processes of the organism, and to connect with these all its functions. 'The means of treating in a scientific manner the phenomena of mind' are completely wanting, inasmuch as these phenomena cannot be brought into relation with any of our scientific conceptions. Physiology must here, therefore, provisionally limit herself to the investigation of the organs with which they are connected. Even of the remaining tasks of the science, the solution of which we may venture to designate as possible, but a few have been really accomplished.

It is difficult to follow a strictly logical course in the exposition of the facts which have been already discovered. Seeing that our knowledge of the relation between the chemical processes and the forces of the organism is so limited that it is nearly all included under the general observations which have already been made, it would be vain to attempt to expound them in their natural and close mutual relations. It is more convenient, therefore, to consider in two distinct parts of this work the *Material exchanges* and the *Transformations of Energy* of the organism. But here a fresh difficulty arises out of the mutual relations of the organic processes. The forces of the organism are often employed in directing its matter, so that a knowledge of these forces is requisite, in the first place, for the proper understanding of the material circulation. Hence it happens that even in the First Part of this

book, which treats of the Exchanges of Matter, reference is often made to movements, therefore to energy which has become kinetic, though, naturally, no reference is made to its origin. Conversely, our knowledge of the characteristic changes in the matter of some organs of work is so limited, that, for many reasons, it is more convenient to state what has been discovered concerning it in the Second Part, when treating of the *Organs of Work* (e.g. the muscles).

The Third Part of this book treats of the Physiology of the *Liberating Organs*—i.e. of the Nervous System. The Fourth Part discusses the origin, development, the periodic changes, and the death of the organism.

PART I.

THE EXCHANGES OF THE MATTER OF THE ORGANISM.


INTRODUCTION—CHEMICAL CONSTITUENTS OF THE HUMAN BODY.

Elements.

THE following elements enter into the composition of the human body: oxygen, hydrogen, carbon, nitrogen, sulphur, phosphorus, chlorine, fluorine, silicon;—potassium, sodium, calcium, magnesium, iron, manganese.

Copper and lead are found as occasional, and, very probably, unimportant constituents. (The supposed discovery of the former metal has probably been owing to the use of reagents containing copper, Lossen.) Probably other universally diffused metals, as lithium, are present, in minute quantities, in the body.

Only a few of the above-mentioned elements occur in a free condition¹ in the body, namely:

1. Oxygen O_2 , $O=O$, enters the body in a free state, and serves to oxidize, or burn, the substances which enter into its composition. For reasons which will be subsequently given, some have falsely surmised that it is in its condition of ozone, O_3 , $-O-O-O-$ or , that oxygen is able to effect these oxidations without the aid of a high temperature. Oxygen is found in all the fluids of the body, either in a state of simple solution or loosely combined.

The existence of a third modification of oxygen, 'antozone,' concerning whose properties statements differ, is now denied, and the phenomena ascribed to it are explained by the presence of hydric peroxide.

2. Nitrogen N_2 , $N\equiv N$ is absorbed from the atmosphere in a free condition, and is consequently found dissolved in the fluids

¹ It must be remembered that even elements in a so-called free condition are combinations of several atoms, e.g. Oxygen, O_2 ; Ozone, O_3 ; Nitrogen, N_2 .

of the body. In addition, it is probably set free in the oxidation of nitrogenous organic compounds, and eliminated, in this condition.

Even Hydrogen, H_2 , occurs in the alimentary canal as a product of decomposition; probably it originates in the butyric acid fermentation.

Chemical Compounds.

The formation of chemical compounds from their elements or from more simple compounds, by so-called synthetic processes, has hitherto only been discovered to occur in the body to a very slight extent. The more accurately-known chemical processes of the body consist, on the contrary, chiefly in the falling to pieces of complicated compounds, whose *composition* is only partially known, and whose *constitution* is entirely unknown to us; these bodies contain carbon, hydrogen, and oxygen; many contain, in addition, nitrogen; some also sulphur, phosphorus, and iron. The most important agent in bringing about this falling to pieces is the oxygen which enters the body in respiration, under whose influence complicated bodies split up into more simple ones, which contain more oxygen, and which are called oxidation-products. The simplest products which arise in this way are carbonic acid, sulphuric acid, phosphoric acid, and water; when these substances are formed, the individual elements combine with as much oxygen as they can in general take up. Nitrogen never separates in combination with oxygen, but it either isolates itself entirely and is then excreted in a gaseous form—an occurrence which has not been absolutely proved—or it leaves the body in simple combinations, *e.g.* as ammonia, or as ammoniacal compounds (ammonias whose hydrogen is replaced by other atomic combinations) like urea.

Between these simple combinations which the organism throws off, and the complex bodies which it receives, there exist a very large number of intermediate substances, which form the principal constituents of the body.

The most thoroughly known of these substances are those whose chemical constitution is most simple; in other words, which are soonest to be eliminated. In the latter we can with tolerable accuracy follow the course of the oxidation and the gradual simplification of the combinations; many of these compounds can be obtained by the oxidation of the substances which precede them, and conversely many of the more simple compounds can be synthetically obtained from their elements. The origin of the more complicated and little known compounds cannot, however, with equal certainty, be referred to oxidation, and it is possible (nay, to a certain extent, probable) that in their production synthetic processes come into play.

A number of substances which enter the body do not undergo such changes as have been alluded to, but pass through it without any change taking place in the grouping of the atoms which compose them. These so-called inorganic matters play a part in the body which is not yet thoroughly known. The chief of these, *water*, serves in the body as the general solvent: it forms, in so far as regards bulk, the chief constituent of all the organs but the bones, and it is received into, and separated from, the body in large quantities, a small quantity being actually formed by oxidation in the body.

The other inorganic matters are the so-called inorganic salts. They also occur in all parts of the body, but (except in the bones, which are composed mainly of salts) only in small quantity; when the tissues of the body are burned these salts remain as 'ashes.' Their importance in the organism is only imperfectly understood. In great part they appear to be not merely simply dissolved, but to form unknown chemical compounds with the more complex, organic constituents. We can only thus explain the constant relation which they bear to other substances (*e.g.* in the bones) and the fact that the solubility and behaviour of certain bodies (*e.g.* the albuminous bodies) depend very much upon the salts which accompany them. Our knowledge of the salts which are really present in the organism is, moreover, still very incomplete, seeing that chemical analysis of the ashes only acquaints us with the acids and metals, but not with the salts which they contain; and, further, a portion of the acids, which occur in the ashes, are only formed in the process of combustion (*e.g.* phosphoric, sulphuric, and carbonic acids).

Amongst the salts which are found in the excreta there are some which have not entered the body in the food, but which originate within it. This is the case with carbonates, sulphates, and phosphates.

The chemical compounds which occur in the animal body will in the work be grouped into the following classes:—

1. Water.
 2. Acids and salts.
 3. Alcohols.
 4. Ethers and anhydrides.
 5. Ammonia and ammoniacal derivatives.
 6. Complex bodies of unknown constitution.
-

1. WATER.

Water H_2O $\text{H}-\text{O}-\text{H}$, as has already been remarked, is a general solvent, and one of the chief constituents of all the juices and tissues of the body (it forms about 70 per cent. of the whole body). It is continually being taken into the body in large quantities with the food, and continually being excreted; small quantities are formed in the body by the oxidation of the hydrogen of organic compounds.

Peroxide of Hydrogen, HO $\text{H}-\text{O}-$ or H_2O_2 $\text{H}-\text{O}-\text{O}-\text{H}$, has been supposed by some to occur in the body, and to play a part in the oxidation-processes which go on within it.

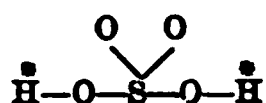
2. ACIDS AND SALTS.

The following acids exist, in part free, in part in salts, in part as constituents of complex compounds to be afterwards alluded to (ethers, amido-compounds).¹

a. Inorganic Acids (i.e. containing no Carbon).

1. Hydrochloric Acid HCl $\text{Cl}-\text{H}^*$ exists in a free state in the gastric juice (perhaps as a more complex acid compound). Its salts (chlorides) are widely diffused throughout the body, *e.g.* sodium chloride, calcium chloride, &c.

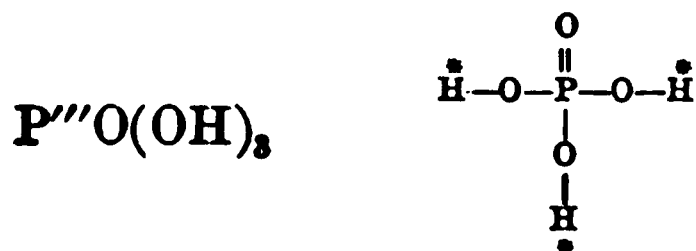
2. Sulphuric acid $\text{S}''\text{O}_2(\text{OH})_2$



occurs in the body in salts (neutral sodium sulphate, calcium sulphate), and in more complex compounds (see Taurine, Albuminous Bodies).

The acid secretion of *Dolium galea* contains free sulphuric acid (De Luca and Panceri, 'Comptes Rendus,' 1867, p. 577).

3. Phosphoric acid (common, tribasic or ortho-phosphoric acid)



¹ In the graphic formulæ of acids which follow, those hydrogen atoms which are replaceable by metals are indicated by an appended asterisk; according to the number of these asterisks the acid is mono, di-, or polybasic.

occurs in salts, as neutral and acid potassium and sodium phosphates, basic calcium phosphate, basic magnesium phosphate, phosphate of magnesium and ammonium (PO_4MgNH_4), and frequently in more complex compounds (see Glycerin-phosphoric Acid, Lecithin).

4. Silicic acid SiO_2 , $\text{o}=\text{Si}=\text{o}$ has been found in some tissues of the body, perhaps only as an accidental constituent, through the inhalation of sand dust.

b. Organic Acids.

5. Fatty acids (general formula $\text{C}_n\text{H}_{2n-1}\text{O}(\text{OH})$.)

The series of fatty acids at present known includes:

Formic acid	. .	$\text{CHO}(\text{OH})$	$\begin{array}{c} \text{O} \\ \parallel \\ \text{H}-\text{C}-\text{O}-\text{H} \\ \\ \text{H} \end{array}$
Acetic acid	. .	$\text{C}_2\text{H}_3\text{O}(\text{OH})$	$\begin{array}{c} \text{O} \\ \parallel \\ \text{H}-\text{C}-\text{C}-\text{O}-\text{H} \\ \quad \\ \text{H} \quad \text{O} \end{array}$
Propionic acid	. .	$\text{C}_3\text{H}_5\text{O}(\text{OH})$	$\begin{array}{c} \text{O} \\ \parallel \\ \text{H}-\text{C}-\text{C}-\text{C}-\text{O}-\text{H} \\ \quad \quad \\ \text{H} \quad \text{H} \quad \text{O} \end{array}$
Butyric acid	. .	$\text{C}_4\text{H}_7\text{O}(\text{OH})$	$\begin{array}{c} \text{O} \\ \parallel \\ \text{H}-\text{C}-\text{C}-\text{C}-\text{C}-\text{O}-\text{H} \\ \quad \quad \quad \\ \text{H} \quad \text{H} \quad \text{H} \quad \text{O} \end{array}$
Valerianic acid	. .	$\text{C}_5\text{H}_{10}\text{O}_2$	
Caproic acid	. .	$\text{C}_6\text{H}_{12}\text{O}_2$	
Oenanthylic acid	. .	$\text{C}_7\text{H}_{14}\text{O}_2$	
Caprylic acid	. .	$\text{C}_8\text{H}_{16}\text{O}_2$	
Pelargonic acid	. .	$\text{C}_9\text{H}_{18}\text{O}_2$	
Capric acid	. .	$\text{C}_{10}\text{H}_{20}\text{O}_2$	
Laurostearic acid	. .	$\text{C}_{12}\text{H}_{24}\text{O}_2$	
Myristic acid	. .	$\text{C}_{14}\text{H}_{28}\text{O}_2$	
Palmitic acid	. .	$\text{C}_{16}\text{H}_{32}\text{O}_2$	
Margaric acid	. .	$\text{C}_{17}\text{H}_{34}\text{O}_2$	(probably a mixture of $\text{C}_{16}\text{H}_{32}\text{O}_2$ and $\text{C}_{18}\text{H}_{36}\text{O}_2$)
Stearic acid	. .	$\text{C}_{18}\text{H}_{36}\text{O}_2$	
Arachidic acid	. .	$\text{C}_{20}\text{H}_{40}\text{O}_2$	

These monobasic acids form a 'homologous' series; their boiling point rises 19°C . with every addition of CH_2 ; those which contain less carbon are fluid and volatile, those which contain more carbon are solid and not volatile. The latter are obtained from the former, by oxidation, CH_2 being removed (carbonic acid and water being formed).



Free fatty acids are frequently found in the analysis of the constituents of the body; yet their presence during life has not been positively determined. The solid fatty acids occur sometimes

in a crystallized condition within cells which previously contained fats. Alkaline salts of the fatty acids (soaps, soluble in water), further amido-compounds (see below Glycine, Leucine), and chiefly certain *ethereal* compounds of the fatty acids (called Neutral Fats) occur in many of the constituent parts of the body. The fatty acids are in addition constituents of still more complicated compounds (see Lecithin).

6. *Glycollic Acids* (general formula $C_nH_{2n-2}O(OH)_2$).

The glycollic acids are derived from the fatty acids by oxidation, by the substitution of one H-atom by OH; even the H of the OH can be replaced by a metal, so that these acids are dibasic.

From those fatty acids which contain more than two carbon atoms (viz. from propionic acid upwards) several isomeric glycollic acids can be obtained, according to the carbon atom to which the second OH group adds itself; thus arise, for instance, the two isomeric lactic acids (oxypropionic acids), which differ in their salts.

The following are the glycollic acids as yet known :

Carbonic acid (oxyformic acid)	$CO(OH)_2$	$\begin{array}{c} O \\ \\ H-O-C-O-H \\ \\ H \end{array}$
Glycollic acid (oxyacetic acid)	$C_2H_2O(OH)_2$	$\begin{array}{c} O \\ \\ H-O-C-C-O-H \\ \\ H \end{array}$
Lactic acid (oxypropionic acid)	$C_3H_4O(OH)_2$	
Sarcolactic acid		$\begin{array}{c} H & H & O \\ & & \\ H-O-C-C-C-O-H \\ & & \\ H & H & \\ & & \\ H & H & O \\ & & \\ H-C-C-C-O-H \\ & & \\ H & O & \\ & & \\ & H & \end{array}$
Ordinary lactic acid		
Butylactic acid (oxybutyric acid)	$C_4H_8O_3$	
Valerolactic acid (oxyvalerianic acid)	$C_5H_{10}O_3$	
Leucic acid (oxycaproic acid)	$C_6H_{12}O_3$	

Of these acids only carbonic and the two lactic acids occur in the organism; glycollic and leucic acids (oxyacetic and oxycaproic acids) are obtained from glycine (amido-acetic acid) and leucine (amido-caproic acid), by the action of nitrous acid.

Carbonic acid.—Carbonic acid as it has been represented in the above graphic formula does not exist in a free state; we are only acquainted with its anhydride CO_2 , $O=C=O$.

Carbonic acid occurs either in the free state (as absorbed gas), in the form of neutral and acid salts, or in amido-compounds such as Urea, in nearly all the component parts of the body, and is excreted in all these forms in large quantities as the principal oxidation-compound of the body. The carbonates which occur in

the ash, are generally, in part, produced during the process of ignition. The most important carbonates found in the body are, sodium carbonate, acid sodium carbonate (Na_2CO_3 and NaHCO_3), calcium carbonate (CaCO_3), and magnesium carbonate (MgCO_3).

Lactic acid.—Of the four isomeric lactic acids at present known, at least two occur in the body; these are—1. common lactic acid, or α oxypropionic acid, and, 2. paralactic or sarcolactic acid.

1. ORDINARY LACTIC ACID (α oxypropionic acid).—This variety of lactic acid exists in the gastric juice, and in the intestinal contents. It is developed when milk turns sour, or is curdled by rennet, and occurs as a product of a peculiar 'lactic' fermentation of gum, starch, sugar, and other vegetable products.

It is most conveniently prepared by dissolving cane sugar and a little tartaric acid in boiling water, and adding, after some days, a mixture of sour milk, putrid cheese, and zinc oxide. In the process of decomposition, which occurs if the temperature be maintained at about 30° or 35° , the cane sugar is decomposed and gives rise to lactic acid, which combines with zinc to form a sparingly soluble zinc lactate, which falls to the bottom of the fluid. The zinc lactate is dissolved in boiling water, purified by crystallization, dissolved in water, and then decomposed with sulphuretted hydrogen; the aqueous solution of the acid is concentrated by evaporation, and then dissolved in ether, which on evaporation leaves it as a syrupy acid fluid.

Lactic acid is a syrupy non-volatile fluid, of specific gravity 1.215, which is odourless and colourless, and possesses a strong sour taste.

Lactic acid forms salts which are all of them soluble in water, the zinc salt being the least so. The lactates of the alkaline metals, as well as the lactates of barium, aluminum, and tin, are not crystallizable; the rest crystallize readily.

The three most characteristic salts are:

Calcium lactate $(\text{C}_3\text{H}_5\text{O}_3)_2\text{Ca} + 5\text{H}_2\text{O}$ crystallizes in the form of white nodular masses. When examined microscopically, calcium lactate is seen to crystallize in tufts of needles. It is soluble in 9.5 parts of cold water.

Zinc lactate $(\text{C}_3\text{H}_5\text{O}_3)_2\text{Zn} + 3\text{H}_2\text{O}$ readily crystallizes in the form of nodular groups of needles; its fundamental forms are vertical prisms with plain faces, or right square prisms.

Lactate of zinc is soluble in six parts of boiling water, and in fifty-eight parts of cold water; it is insoluble in alcohol.

2. PARALACTIC OR SARCOLACTIC ACID occurs in the muscular juice, and is the cause of the acid reaction which is developed when muscle becomes fatigued, or passes into rigor.

Sarcolactic acid possesses physical properties which are nearly identical with those of lactic acid; it is distinguished from the latter—1. by its products of oxidation; 2. by the amount of water of crystallization of its salts; 3. by their solubility; 4. by the action which it exerts on polarized light.

The essential characters which serve to distinguish sarcolactic from common lactic acid are exhibited in the following tabular statements:—

Lactic Acid.

Its calcium salt has the formula $(\text{C}_3\text{H}_5\text{O}_3)_2\text{Ca} + 5\text{H}_2\text{O}$; this salt contains 29.22 per cent. of water. It is soluble in $9\frac{1}{2}$ times its weight of cold water.

Sarcolactic Acid.

The calcium salt has the formula $(\text{C}_3\text{H}_5\text{O}_3)_2\text{Ca} + 4\text{H}_2\text{O}$; it contains 24.82 per cent. of water. Is soluble in 12.4 times its weight of cold water.

Lactic Acid.

The zinc salt has the formula $(C_3H_5O_3)_2 Zn + 3 H_2O$; it contains 18·17 per cent. of water. It is soluble in fifty-eight parts of cold water. It is most sparingly soluble (or insoluble) in alcohol. Is optically inactive.

When oxidized by means of potassium bichromate and sulphuric acid, it yields formic and acetic acids.

Sarcosylactic Acid.

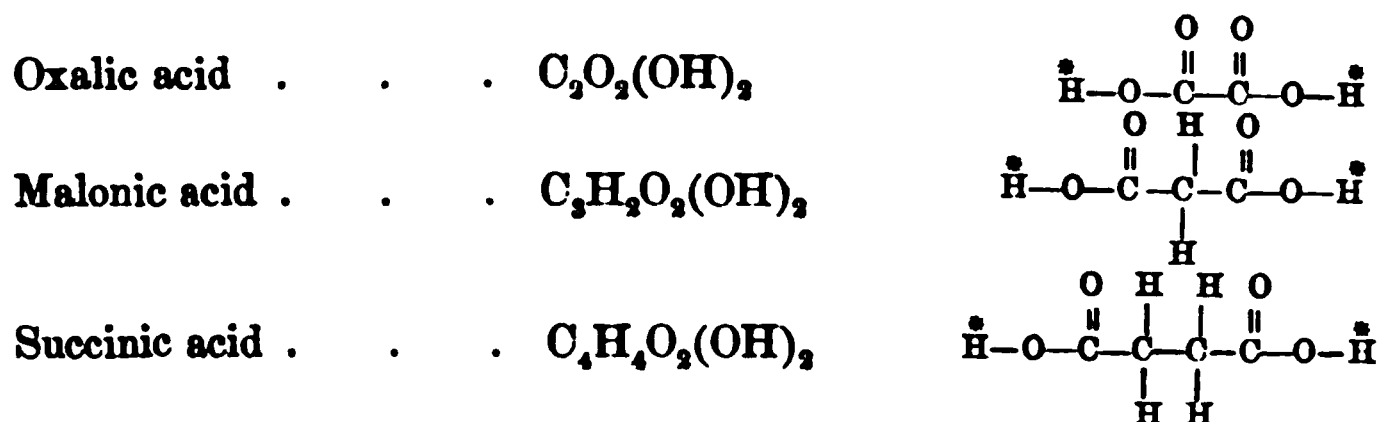
The zinc salt has the formula $(C_3H_5O_3)_2 Zn + 2 H_2O$; it contains 12·90 per cent. of H_2O . Is soluble in six parts of cold water. Is soluble in 2·2 parts of alcohol. Specific rotatory power = $-7^{\circ}65$.

When oxidized by means of potassium bichromate and sulphuric acid, it yields malonic acid.

Sarcosylactic acid can be obtained from the juice of flesh by the following method. Finely divided flesh is treated with cold water, the watery extract is boiled; after separating the coagulum, the solution is precipitated with solution of barium hydrate. After separating the precipitate which this reagent occasions, a stream of carbonic acid is passed through the fluid, so as to precipitate the excess of barium which remains. After filtration the solution is concentrated by evaporation until it assumes the consistence of a syrup. It is then acidified with sulphuric acid, and shaken up with ether, which dissolves the sarcosylactic acid, and from the solution in which, it is obtained on spontaneous evaporation. The sarcosylactic acid thus obtained is purified by converting it into one of its salts, crystallizing, &c.

7. Oxalic Acids (general formula $C_nH_{2n-4}O_2(OH)_2$).

These are dibasic acids obtained by the oxidation of the fatty or glycollic acids (H_2O being removed). The members of the series which have to be considered here are the following:



Of these, oxalic acid, and perhaps succinic acid (although this has been lately disputed), occur in the organism in the form of salts.

Oxalic acid.—The only salt of oxalic acid which is known to occur in the body is calcium oxalate CaC_2O_4 , which frequently is deposited in very small quantities from the urine in the form of a very scanty sediment, which exhibits microscopic octahedra belonging to the cubical system. These crystals, when present, are found mixed with the ‘mucous cloud’ which falls from urine when it is left undisturbed. Calcium oxalate is occasionally the chief constituent of urinary calculi; it is found occasionally in the gall-bladder and in the faeces.

Succinic acid has been found in the fluid of hydatid cysts, in the juice of glandular organs, in the blood, and in the urine. According to Meissner, this acid may be formed in the system from substances such as tartaric and malic acids, which yield it when they are reduced, or by the oxidation of fats and other vegetable products.

Succinic acid is a white crystalline solid, readily soluble in cold water, still

more so in hot water; it is very scantily soluble in cold alcohol. It melts at 175° or 180° , and volatilizes without undergoing decomposition.

To separate succinic acid from urine the following process may be adopted : the urine is precipitated with baryta water ; the excess of baryta is removed from the filtrate by the cautious addition of sulphuric acid, and the fluid is then concentrated by evaporation until the urea begins to crystallize. It is then cooled, the liquid is separated by filtration from the solid matters which have separated, and to the filtrate a very large excess of pure alcohol is added. This causes a precipitate to fall which contains sodium succinate, mixed with many organic and inorganic substances. From this mixture the salt is separated by dissolving in water and crystallizing. The crystals of sodium succinate may be decomposed by means of hydrochloric acid, and the liberated succinic acid is then dissolved in a mixture of alcohol and ether, and crystallized. Succinic acid crystallizes in the form of oblique prisms, with a rectangular base. - The acute angles of the prism are sometimes truncated, and the appearance of the crystals is then that of irregular hexagonal tables.

8. *Oleic Acids* (general formula $C_nH_{2n-2}O(OH).$)

These monobasic acids may be represented as fatty acids, in which two of the carbon affinities are not saturated (at least by H). Some of the members of the series are:

Acrylic acid	$C_3H_3O(OH)$	$ \begin{array}{c} H & H & O \\ & & \\ H-C & -C & -C-O-H^* \\ & & \\ & & \end{array} $
Crotonic acid	$C_4H_5O(OH)$	or
Angelica acid	$C_5H_7O(OH)$	$ \begin{array}{c} H & H & O \\ & & \\ H-C & -C & -C-O-H^* \\ & & \end{array} $
Oleic acid	$C_{18}H_{33}O(OH)$	$ \begin{array}{c} H & H & O \\ & & \\ H-C & -C & -C-O-H^* \\ & & \end{array} $

Of these acids only oleic acid occurs in the body, and when it does so it is in the same compounds as those of the fatty acids—viz., as a soap, as a neutral fat (olein), or in lecithin.

OLEIC ACID is at temperatures below 14° a colourless, tasteless, odourless, non-volatile, oily fluid, which does not possess an acid reaction. It is scarcely soluble in water, but is easily soluble in alcohol and ether.

Fuming nitric acid converts oleic acid into a crystalline solid body, melting at 145° , which is isomeric with it—viz., elaidic acid.

When subjected to destructive distillation oleic acid gives rise to sebacic acid $C_{10}H_{18}O_4$; the latter occurs in small pearly needle-shaped crystals, often united in groups. It melts at 127° or 128° .

The alkaline salts of oleic acid are soluble in water; the solution is precipitated by acetate of lead (lead-plaster); the oleate of lead is, when dried, a white powder; it is distinguished from the lead salts of the fatty acids by its solubility in ether.

9. *Biliary Acids.*

As is implied by the name, the acids belonging to this group occur in the biliary secretion of animals, or are products of decompositions of acids found in the bile. They are of more complex and less known constitution than the acids which have been previously considered. They are insoluble in water, but form easily-soluble soap-like alkaline salts, and possess a common and characteristic reaction—viz., when the acids themselves, or their

Glycocholic acid may also be separated from taurocholic acid by precipitating a solution containing the mixed acids by means of lead acetate, when lead glycocholate falls, leaving nearly all the taurocholic acid in solution. From its lead salt glycocholic acid may be separated by decomposing with sulphuretted hydrogen, &c.

Glycocholic acid crystallizes in fine white needles, possessed of the combined bitter and sweet taste which is characteristic of bile; it is soluble with difficulty in cold, but more easily soluble in hot water. It is readily soluble in pure alcohol, but only very sparingly soluble in ether.

It forms soluble compounds with the alkalies, which are precipitated by solution of lead acetate, the lead precipitate being soluble in hot alcohol, from which it is deposited when the liquid cools. Solutions of the alkaline salts of glycocholic acid possess the power of holding in solution small quantities of the neutral fats.

Glycocholic acid deviates the ray of polarized light to the right. The specific rotatory power of the alcoholic solution = $+29^{\circ}$.

When boiled for many hours with solutions of caustic alkalies or with dilute hydrochloric or sulphuric acids, glycocholic acid combines with the elements of water, and yields glycocine $C_2H_5NO_2$, and an acid common to it and taurocholic acid, called cholic acid $C_{24}H_{40}O_5$.

Taurocholic acid $C_{26}H_{45}NSO_7$ is the principal bile-acid occurring in human bile, in which, however, it is accompanied by glycocholic acid; it is the sole ingredient in the bile of purely carnivorous animals.

From dogs' bile this acid can be prepared by following the method previously recommended for the separation of glycocholic acid from the bile of the ox.

It is separated from mixtures in which it coexists with glycocholic acid by precipitating them first of all with normal lead acetate (which precipitates the glycocholic acid but leaves taurocholic acid in solution), and afterwards with a solution of basic lead acetate, followed by a little ammonia. The lead taurocholate which falls under these circumstances is decomposed with sulphuretted hydrogen and taurocholic acid set free.

Taurocholic acid can be obtained, though not so readily as glycocholic acid, in the form of needle-shaped crystals, which are highly deliquescent; it is readily soluble in water and alcohol, but is insoluble in ether. It possesses a bitter-sweet taste similar to that of glycocholic acid. Its alcoholic solutions are dextrigyrus; their specific rotation = $+25^{\circ}$.

Solutions of taurocholic acid, or of the taurocholates, in the presence of decaying animal matter, readily decompose, taurine

being set free. When boiled for a long time with solution of the caustic alkalies they split up into taurine and cholic acid—



Cholic acid (syn. cholalic acid) $\text{C}_{24}\text{H}_{40}\text{O}_5$ is a product of the decomposition of glyco- and taurocholic acid by acids and alkalies. It occurs as a constant, though scanty, ingredient in the intestinal contents, and is said to be present in the urine in icterus.

Cholic acid may be prepared either from the purified bile acids or directly from bile. In the latter case the bile is boiled for about a day with a saturated solution of baryta water, and then precipitated by means of hydrochloric acid. The impure cholic acid is washed with water and dissolved in a solution of caustic potash; a little ether is added, and then an excess of hydrochloric acid. After some days cholic acid separates in a crystalline form. It may be purified by recrystallization from alcohol.

Cholic acid occurs both in the amorphous and crystalline condition. It crystallizes from hot alcoholic solutions in the form of tetragonal octohedra or in tetrahedra, which contain water of crystallization. From solutions in pure alcohol the acid separates in prisms, which contain no water of crystallization.

The solubility of cholic acid in various liquids varies according to its state. The amorphous acid is sparingly soluble in water, more soluble in ether, and very soluble in alcohol. The crystalline acid is insoluble in water, sparingly soluble in alcohol and little soluble in ether (Hoppe-Seyler).

Cholic acid and its salts exert right-handed rotation on polarized light. The rotatory power of its alkaline salts in alcoholic solution is independent of the concentration of the solution; that of the sodium compound = $+31^\circ.4$.

Choloidic acid $\text{C}_{24}\text{H}_{38}\text{O}_4$ only differs from cholic acid in elementary composition by containing 1 molecule less of H_2O . It is obtained by heating cholic acid to 195° , or by boiling it for some time in strong hydrochloric acid; it appears to be an intermediate product in the formation of dyslysin. Choloidic acid is amorphous; it is insoluble in water, sparingly soluble in ether, and readily soluble in alcohol.

Dyslysin $\text{C}_{24}\text{H}_{36}\text{O}_2$ is obtained by the continued action of boiling mineral acids upon any of the preceding bile acids, or by heating choloidic acid to 295° .

It is an amorphous substance, insoluble in water and alcohol, and very sparingly soluble in ether. When boiled with alcoholic solution of potash it is reconverted into cholic acid.

Glyco-hyochohic acid $\text{C}_{27}\text{H}_{43}\text{NO}_6$ and tauro-hyochohic acid $\text{C}_{27}\text{H}_{45}\text{NSO}_6$ are the bile acids which occur in pigs' bile. These conjugated acids only differ from the normal bile acids of other

animals in that hyocholic acid $C_{25}H_{40}O_4$ takes the place of cholic acid. The latter can be obtained from pig's bile by following the process mentioned for the preparation of cholic acid $C_{25}H_{40}O_5$.

By boiling with hydrochloric acid, hyocholic acid is converted into an anhydride, hyodyslysin $C_{25}H_{38}O_3$.

Chenotaurocholic acid ($C_{29}H_{51}NSO_7$?) is the biliary acid which occurs in the bile of the goose. It is amorphous; is soluble in water and alcohol. It is abundantly precipitated by basic lead acetate. By boiling with alkaline solutions or acids, it yields taurine and chenocholic acid $C_{27}H_{44}O_8$; this acid is said to be crystallizable, scantily soluble in ether and alcohol, and insoluble in water.

Guanogallic acid is an amorphous, non-nitrogenous biliary acid contained in the Peruvian guano.

Lithofellic acid $C_{20}H_{36}O_4$ is almost the only constituent of bezoar stones; these are stated to be biliary calculi, occurring in a species of antelope. If the powdered stone be treated with boiling alcohol this acid is extracted, and deposited in a crystalline form.

Pettenkofer's reaction.—As has been stated in a previous paragraph, it is a character common to all the biliary acids and their derivatives to give a violet colour when they are gently heated with sugar and sulphuric acid. As the reaction is one of importance, the conditions necessary to its development must be examined.

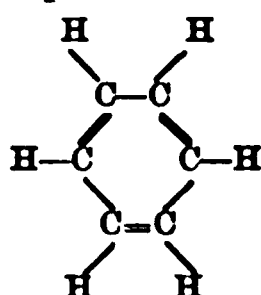
The bile acid, or compound of the bile acid, to be tested may be either in the liquid or solid condition. If in solution, a drop of a strong solution of cane-sugar is added to it, and then pure sulphuric acid is gradually poured in, care being taken that the temperature does not rise above 70° , although it is desirable that this temperature be reached. A cherry-red colour is developed, which afterwards assumes a purple tint. If the substance to be treated be solid, it is moistened with a weak solution of cane-sugar, sulphuric acid is added, and a gentle heat applied; the beautiful colour develops after a short interval.

Other substances, *e. g.* albuminous bodies and fats, give reactions with sugar and sulphuric acid, which resemble somewhat that of biliary acids; it is therefore important that these should be separated before applying Pettenkofer's test.

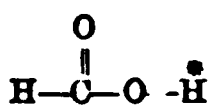
The spectrum of the red fluid obtained by acting upon bile acids with sugar and sulphuric acid is confirmatory of their presence. It is marked by two absorption bands; one of these is situated between E and F, a second between D and E. The red-coloured fluid which is produced by albuminous substances when treated with sugar and sulphuric acid exhibits only one absorption band, situated between E and F.

10. *Aromatic Acids.*

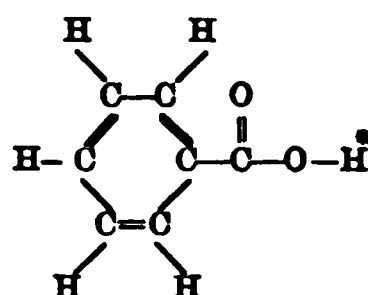
These are acids which are derived from the atomic group benzol C_6H_6 . In this very stable group each H-atom can be replaced by a monatomic atom or group of atoms; amongst others by the fatty acids. We may explain the relations of benzol by saying that the monatomic group phenyl C_6H_5 ($= C_6H_6 - H$) can replace one atom of hydrogen in a large number of combinations.



C_6H_6
Benzol



CH_2O_2
Formic acid



$CH(C_6H_5)O_2$
Phenyl-formic or Benzoic acid

The following are aromatic acids which possess some physiological interest:—

Benzoic acid (Phenyl-formic acid)	$CH(C_6H_5)O_2$
Chlorobenzoic acid (Chlorophenyl-formic acid)	$CH(C_6H_4Cl)O_2$
Salicylic acid (Oxyphenyl-formic acid)	$CH(C_6H_4[OH])O_2$
Anisic acid (Methoxyphenyl-formic acid)	$CH(C_6H_4[O.CH_3])O_2$

These acids do not occur as regular constituents of the body, yet they pass through it after having been introduced as constituents of vegetable food, and in the body form peculiar compounds (see Hippuric Acid). Possibly they also form part of more complex bodies, as of Tyrosine, which is closely related to them, and which is a product of the decomposition of the albuminous substances.

Benzoic Acid $C_7H_5O(OH)$.—This acid occurs occasionally as a constituent of the urine of herbivorous animals; it is generated in large quantities when the urine of the herbivora decomposes, being then a product of the breaking up of hippuric acid (*q.v.*)

Benzoic acid is a white crystalline body, which melts at about 121° and boils at 249° . It is very sparingly soluble in cold water, more easily soluble in boiling water (1 in 25), and is very soluble in alcohol. It crystallizes when sublimed in the form of rectangular plates. Benzoic acid combines with metals to form salts which are generally soluble. Ferric chloride produces in solutions of alkaline benzoates a buff-coloured precipitate of ferric benzoate. When boiled with fuming nitric acid, benzoic acid yields nitro-benzoic acid $C_7H_5(NO_2)O_2$.

When introduced into the system benzoic acid links itself to glycine, and is converted into hippuric acid (benzamidacetic acid).

Separation of Benzoic Acid from Organic Fluids.—The liquid is neutralized, concentrated, and extracted with alcohol, in which alkaline benzoates are soluble. The alcoholic solution is evaporated to dryness, dissolved in a little water, acidulated with sulphuric acid, and shaken with ether, which dissolves benzoic together with many other organic acids which may be present.

The separation of benzoic acid from these is a matter of considerable difficulty. (Consult Hoppe-Seyler's Handbuch, p. 88; Gautier's edition of Gorup-Besanez, pp. 166, 167.)

3. ALCOHOLS.

Alcohols are compounds of certain hydrocarbon radicals (called 'alcohol-radicals') with the group Hydroxyl HO. According to the number of hydroxyls contained in the molecule of the alcohol is it monatomic or polyatomic.

The only proximate principles of the animal body which belong indisputably to the group of alcohols are cholesterin and glycerin; indeed, if we used the term 'proximate principle' in the strictest sense we should have to exclude glycerin, of which only the ethers occur in the organism.

The sugars, being either polyatomic alcohols, or bodies very closely related to them, may be conveniently classed in this group.

Cholesterin $C_{26}H_{43}(OH)$ is a constituent of the nerve centres, of nerves, of the blood and most animal fluids, especially the bile; of the cerumen, of the intestinal contents. It is often found in large quantities in old extravasations, in the pus of chronic abscesses, &c.

Cholesterin is a crystalline body, insoluble in water, dilute acids, and alkalies, but readily soluble in ether and hot alcohol; the latter solvent deposits it on cooling in the form of rhombic tables. It is likewise soluble in chloroform, and to a certain extent in solution of the salts of the bile acids. Dry cholesterin melts at 145° , and distils in vacuo at 360° . Its solutions exert a left-handed rotation on the plane of polarization. The specific rotatory power of solutions of cholesterin = -32° . Amongst the most useful reactions for detecting cholesterin are the following:—

1. When treated with concentrated sulphuric acid, and afterwards a little iodine, a play of colours, of which blue, green, and red are the most prominent, is produced. This reaction may be employed as a more stringent proof than that offered by the microscopic characters of the crystals, and it may well be observed under the microscope.

2. When cholesterin is gently heated with five volumes of sulphuric acid and one volume of water, the edges of the crystals are seen to become of a carmine colour; this reaction admits of being performed on a microscopic slide, and its results of being watched under the microscope.

3. When cholesterin is dissolved in chloroform, and the chloroformic solution is shaken with an equal volume of strong sulphuric acid, the chloroform becomes successively blue, red, cherry-red, and ultimately purple, whilst the subjacent sulphuric acid acquires a marked green fluorescence.

Preparation and Separation of Cholesterin.—From biliary

concretions, in which it is often present in very large quantity, cholesterin is easily prepared. The concretion is powdered, and the powder having been dried, is boiled with alcohol; the alcoholic solution is filtered whilst still hot, and when it cools it deposits cholesterin crystals, which may be further purified by a re-solution in alcohol.

Cholesterin may sometimes be detected in normal products of the body (*e. g.* in cerumen), and often in pathological products (*e. g.* in pus), by its crystalline form and by the reactions which the crystals display with sulphuric acid, or with sulphuric acid and iodine. More commonly, however, it exists in a state of solution, and is found amongst the substances extracted by ether from the solid residue of organic liquids and solids. In the ethereal solution it is usually found mixed with other bodies, and especially with the fats. The process of separation from these consists in boiling the mixed residue left by ether with a solution of caustic potash (usually in alcohol); the fats are thus decomposed, yielding soluble soaps and glycerin. After evaporating any alcohol which the mixture may contain, and extracting with water, the cholesterin will be left, and it may then be dissolved in ether or hot alcohol, and allowed to crystallize.

Glycerin $C_3H_8(OH)_3$.—In all probability glycerin does occur in a free condition in the contents of the small intestines, where it must be present amongst the products of the decomposition of the neutral fats by the pancreatic ferment. Its interest to the physiologist, however, depends upon the fact that the fats of the body are neutral ethers formed by the union of certain acid radicals with the triatomic alcohol now under consideration. The relation of glycerin to the fats is best considered when these are described. The following facts with regard to it may, however, be referred to in this place:—

Pure glycerin is a neutral, colourless, transparent, viscid, hygroscopic fluid, possessed of an intensely sweet taste. It is soluble in all proportions in water and alcohol, but is insoluble in ether. The specific gravity is 1.27. Under a pressure of 50 mm. it boils at 210° , without undergoing decomposition.

The Sugars.

The different sugars are crystalline, soluble bodies, possessed of a sweet taste; their solutions deviate the plane of polarized light. In consequence of the ease with which they are oxidised they reduce many metallic oxides. They split up under the influence of certain organisms (*e.g.* yeast cells), and other so-called ferments into simpler bodies, known as *products of fermentation*, heat being evolved during the process. The different members of the family appear to be very closely related to one another.

The different sugars and their anhydrides are usually designated by the term 'carbo-hydrates,' which merely expresses that, in addition to carbon, they contain hydrogen and oxygen in the proportion in which these elements are contained in water (H_2O). These bodies either contain six atoms of carbon or a multiple of this number. They are divided into three groups:—

1. <i>Saccharoses.</i> $C_{12}H_{22}O_{11}$	2. <i>Glucoses.</i> $C_6H_{12}O_6$	3. <i>Amyloses.</i> $(C_6H_{10}O_5)_n$
+ Cane sugar	+ Grape sugar (dextrose)	+ Starch
+ Milk sugar	— Levulose	+ Glycogen
+ Melitose	+ Galactose	+ Dextrin
+ Melizitose	— Sorbin	— Inulin
+ Mycose	— Eucalin	Gums
Synanthrose	Inosit	Cellulose
		Tunicin

Most of these compounds occur in the vegetable kingdom, forming some of the most important constituents of plants, and a few also occur in the animal organism. The chemical constitution of only a few is known, but that they are nearly related to each other is known by the fact that most of them can be converted into glucose by the action of dilute sulphuric acid. The majority of them are optically active, or possess the power of turning the plane of polarization, some to the right hand and some to the left. The right-handed instances are marked in the preceding table with +, and the left-handed with —.¹

The following sugars occur in the animal body :—

Grape Sugar, Glucose, or Dextrose $C_6H_{12}O_6$ (*synonyms, Diabetic sugar, Liver sugar, Starch sugar*).

The general reactions of this body point to its being an aldehyde of the hexatomic alcohol mannite $C_6H_8(OH)_6$.

Grape sugar is a constituent of the contents of the alimentary canal and of the chyle after a starchy or saccharine diet. It is, besides, a constant constituent, in small quantities, of the blood, the lymph, the liver, and the muscles. It occurs in the hen's egg, before and during incubation; it is found in the liquor amnii and the allantoic fluids. Its existence in normal urine is doubtful, but it occurs in large quantities in the various organic solids and liquids, and especially in the urine of men affected with *diabetes mellitus*, &c.

Dextrose is a white crystalline solid, possessed like other sugars of a sweet taste. It is less sweet and less soluble in water than cane-sugar.

Its aqueous solution rotates the plane of polarization to the right. Its specific R. P. = + 53°·5.

Dextrose reduces ammoniacal solution of salts of silver, precipitating the metal as a brilliant mirror.

By the action of sodium amalgam dextrose is converted into mannite $C_6H_{14}O_6$.

Alcoholic fermentation.—In the presence of the yeast plant, and at temperatures varying between 0° C. and 35° C. (25° to 30° C.

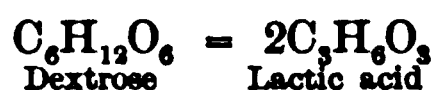
¹ Schorlemmer, *Chemistry of Carbon Compounds*, p. 284.

being most favourable), dextrose undergoes immediately the alcoholic fermentation, of which the chief products are alcohol and carbon dioxide



Although these are the chief products, other bodies are found in smaller quantities, as glycerin and succinic acids.

Lactic fermentation.—In the presence of decomposing albuminous matters, if the temperature be suitable (30° to 35°), and the reaction neutral or alkaline, dextrose is converted into lactic acid; thus—



Reactions of solutions of dextrose.—1. Amongst the most characteristic properties is the capability of undergoing the alcoholic fermentation.

2. When to a solution of dextrose there is added first a solution of copper sulphate, and then a solution of potash hydrate, instead of a precipitate of hydrated copper oxide falling, the fluid becomes of a deep azure-blue colour. On now heating the liquid, it assumes an orange-yellow colour, and there falls a red precipitate of anhydrous cuprous oxide. This is known as Trommer's test.

3. When a solution of dextrose is boiled with a solution of potash hydrate, the fluid assumes at first a sherry colour, which deepens in tint, and ultimately becomes of a deep, reddish-brown colour. (Moore's test.)

Preparation and identification of dextrose.—Dextrose can best be separated from diabetic urine by concentrating, decanting from the insoluble salts which separate during the process, and allowing the syrupy fluid to remain undisturbed for long periods; the glucose then usually separates out in the form of yellow, warty, friable masses. These are freed as much as possible from urea, soluble salts, &c., by being washed with absolute alcohol, and afterwards are dissolved in boiling spirits of wine. This solution will yield crystals of dextrose.

For the identification of glucose its action on polarized light, if possible its specific rotatory power, its capability of undergoing the alcoholic fermentation, and its reaction with alkaline solutions of copper salts, are chiefly relied on.

Sugar of milk $\text{C}_{12}\text{H}_{22}\text{O}_{11} + \text{H}_2\text{O}$ is a constituent of the milk of all mammals. It occurs as a colourless, hard, brittle, crystallized solid; it crystallizes in the form of right rhombic prisms, which are often united in clusters. It is soluble in only six parts of cold water and is insoluble in absolute alcohol. Its specific rotatory power = $+58.2$.

This sugar can *directly* only undergo the lactic acid fermentation, but when boiled with dilute sulphuric acid it is converted into an isomeric sugar called galactose, which ferments with ease. When left in contact with yeast, sugar of milk usually undergoes

the alcoholic fermentation, a formation of galactose being probably the necessary precursor.

Sugar of milk may be obtained by concentrating whey, when it crystallizes out. Its solutions react like solution of dextrose with Trommer's test.

Inosit $C_6H_{12}O_6 + 2H_2O$ is formed in very minute quantities in muscular tissues, especially in that of the heart; it also occurs in the liver, the lungs, the brain, the spleen, and the kidneys.

It is said to be an occasional constituent of the urine in Bright's disease, and occasionally to take the place of sugar in the urine of diabetes.

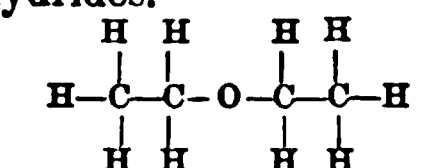
Inosit occurs also in vegetable tissues, especially in green kidney-beans.

Inosit occurs in colourless rhombohedral crystals belonging to the monoclinic system; it is soluble in water, but insoluble in alcohol or ether. Its solution tastes sweet; it does not affect the plane of polarized light, and is incapable of undergoing the alcoholic fermentation. In contact with decomposing animal matters, inosite yields lactic and butyric acids.

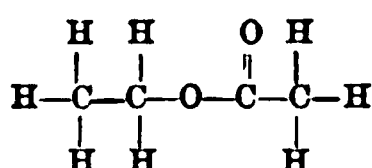
Scherer's test for Inosit.—A fragment of inosit is placed in a platinum capsule and nitric acid is added. Heat is then carefully applied so as to drive off the acid. The residue is treated first with solution of ammonia, and then with calcium chloride. On evaporating cautiously to dryness, a beautiful rose-red colour is developed.

4. ETHERS AND ANHYDRIDES.

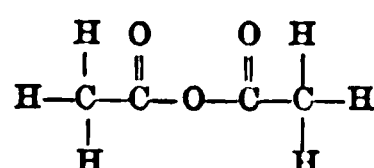
When alcohol-radicals or acid-radicals, or both alcohol and acid radicals, are held together by atoms of oxygen, ethers are formed; when several similar radicals are united together in this fashion, the compounds are called anhydrides.



$C_2H_5.O.C_2H_5$
Diethyl ether (common
ether or alcohol anhydride)

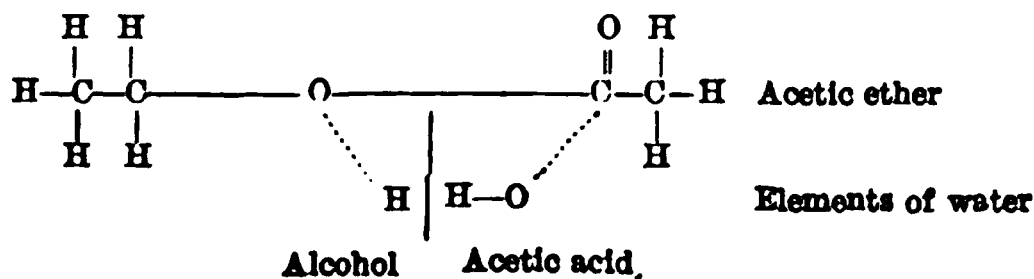


$C_2H_5.O.C_2H_3O$
Acetyl-ethyl ether
(Acetic ether)



$C_2H_3O.O.C_2H_3O$
Diacetyl oxide
(Acetic anhydride)

The ethers and anhydrides are formed from alcohols and acids by a removal of H_2O , and are reconverted into them when they combine with H_2O . The first process is a synthesis, the second a process of decomposition; one may distinguish both these processes from other syntheses and decompositions, by applying to them the term of *hydrolytic*. The part which water plays in them is exhibited by the following diagram, which shows how the action of water leads to the splitting of acetic ether into alcohol and acetic acid.



Hydrolytic decompositions sometimes occur on mere contact with water, at other times under the influence of boiling water (sometimes only at temperatures above that of boiling water, '*superheating*'), or under the influence of boiling water and mineral acids; lastly, they occur at moderate temperatures under the influence of certain ('*hydrolytic*') ferments. The following ethers and anhydrides occur in the body.

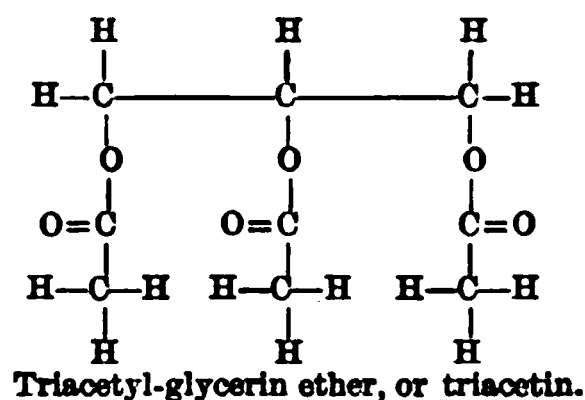
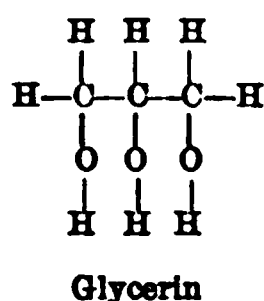
1. Glycerin-Ethers or Glycerides.

a. The Neutral Fats.

The fatty matter of the animal body is mainly composed of a mixture of so-called neutral fats, termed respectively stearin, palmatin, and olein, of which the two former, which are solid bodies, are held in solution, at the temperature of the animal body, by the third, which is liquid at ordinary temperatures.

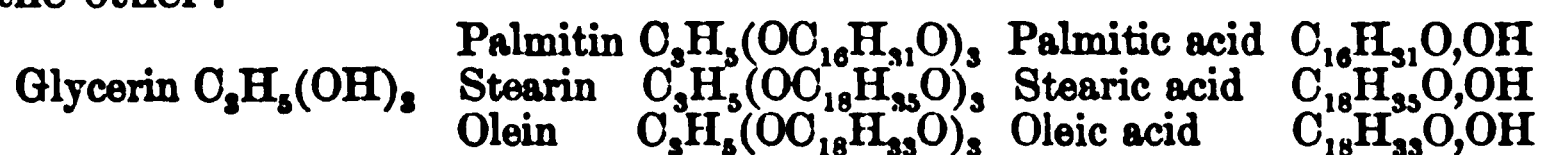
The three neutral fats just named are ethers derived from the triatomic alcohol glycerin $C_3H_5(OH)_3$.

We may form a true conception of the relations of a neutral fat to glycerin by comparing the graphic formula of glycerin with that of an artificial neutral fat, triacetin $C_3H_5(OC_2H_3O)_3$. In glycerin there are three hydroxyls, and the H in any one, or in all, of these may be replaced by the oxidized radical of a fatty acid, *e.g.* by acetyl C_2H_3O ; when all three of the hydrogens are thus replaced the neutral fat called triacetin, which is represented by the appended graphic formula, is formed:—



Now the neutral fats of the animal body are constituted on the same type as triacetin, except that, instead of acetyl, other oxidized acid-radicals replace the H of hydroxyl. In the two more solid fats, viz. stearin and palmitin, the oxidized radicals of stearic and palmitic acids occupy the position of acetyl in the above graphic representation. In the more liquid constituent of the fats, viz. olein, the oxygenized radical of oleic acid replaces the three H's of hydroxyl.

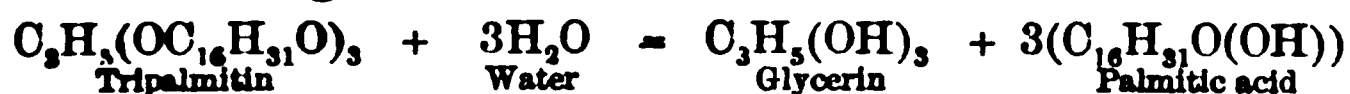
The formulæ of the three principal fats are appended, and their relation shown to glycerin on the one hand, and to these acids on the other:—



In addition to the three neutral fats already mentioned, the

following are contained in milk, and constitute the fat of butter: myristin, caprinin, caprylin, capronin, butyrin.

The neutral fats are fluid (oils) or easily melted, insoluble in water, easily soluble in ether and alcohol; when fluid they render paper transparent (cause *grease spots*); when mixed with *colloid* substances and water, they admit of being broken up into fine drops, so that the fluid becomes white and opaque (emulsion). Under the influence of hydrolytic ferments, or when superheated with water, they combine with the elements of water, glycerin and free fat acids being liberated; thus:—



The rancid smell of decomposing fats is due to volatile acids, which happen to be formed under the circumstances.

When the neutral fats are boiled with solutions of the alkaline hydrates or carbonates, they undergo the process of *saponification*, i.e. they combine with the elements of water, and decompose into glycerin and a fatty acid; the latter constituent combining at once with the alkaline metal to form a soluble salt. Thus when stearin, palmitin, or olein are boiled with potash hydrate, or with sodium hydrate, we have as results of the operation in the first case potassium stearate, palmitate, or oleate, respectively, and glycerin; in the second case there result sodium stearate, palmitate, or oleate, and glycerin.

When boiled with litharge the neutral fats yield an insoluble lead compound and glycerin. The term soap is applied to the metallic salts of the fatty acids, and hence the term saponification is employed to designate the process which results in the formation of these compounds.

The following are some of the more important characters of the three principal neutral fats occurring in the animal body:—

Stearin, or Tristearin, $\text{C}_3\text{H}_5(\text{C}_{18}\text{H}_{35}\text{O})_3\text{O}_3$, is the chief constituent of the more solid fats. Its melting point is higher than that of any other neutral fat, but varies, according to the treatment to which it has been subjected, between 53° and 66° .

It is insoluble in water, but is soluble in hot alcohol, in ether and chloroform. It separates from its solution in hot alcohol in the form of shining rectangular scales.

Palmitin, or Tripalmitin, $\text{C}_3\text{H}_5(\text{C}_{16}\text{H}_{31}\text{O})_3\text{O}_3$, always accompanies stearin in the animal fats.

Its melting point is like that of stearin, not very constant, varying with the treatment it has undergone, but is certainly lower than that of stearin. The mean melting point is about 45° C. Palmitin is insoluble in water; it is more readily soluble in hot alcohol than stearin; it is deposited from its alcoholic solution in the form of needles.

Alcoholic solutions of mixtures of stearin and palmitin

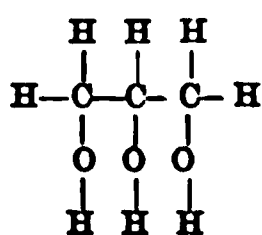
deposit crystals of a mixture or perhaps a compound of the two fats; formerly this mixture was looked upon as an individual fat, called margarin; the supposed margarin usually crystallizes in the form of very fine needles or little plates radially arranged around a point.

Olein, or Triolein, $C_3H_5(C_{18}H_{33}O)_3O_3$, is a colourless body of oily consistence at ordinary temperatures; at -5° it crystallizes in fine needles. Olein is oxidized at ordinary temperatures, and then assumes a more or less yellow colour. It is insoluble in water and readily soluble in *absolute* alcohol and ether.

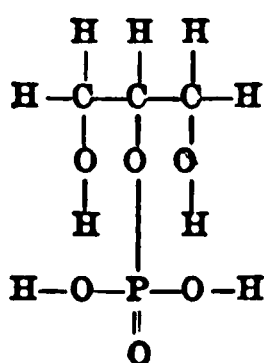
b. Glycerin-phosphoric Acid and its derivatives.

Closely related in chemical constitution to the neutral fats is a body possessed of great interest, from its connection with the chemistry of the more complex constituents of the nerve-centres, viz. glycerin-phosphoric acid $C_3H_5PO_6$. This body may be looked upon as an acid glycerin-ether, derived from glycerin and orthophosphoric acid.

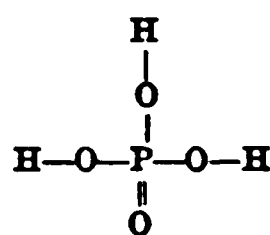
By studying the appended graphic formulæ of glycerin, phosphoric acid and glycerin-phosphoric acid, the reader will readily apprehend the view which we take of the constitution of glycerin-phosphoric acid.



$C_3H_5(OH)_3$
Glycerin



$C_3H_5(OH)_2O.PO(OH)_3$
Glycerin-phosphoric acid



$PO(OH)_3$
Orthophosphoric acid

Glycerin-phosphoric acid is readily prepared by mixing phosphorus pentoxide and glycerin, avoiding any great rise in temperature. The mixture is heated for some days at a temperature not exceeding 100°C , and from the mixture of glycerin, phosphoric acid and glycerin-phosphoric acid the latter is separated by various processes. It is one of the most important products of the decomposition of lecithin; indeed, as will be shown in the sequel, lecithin may be looked upon as a direct derivative of glycerin-phosphoric acid.

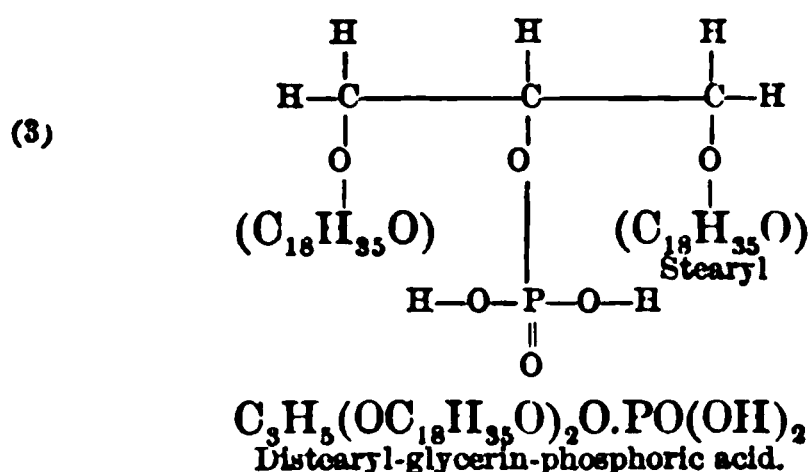
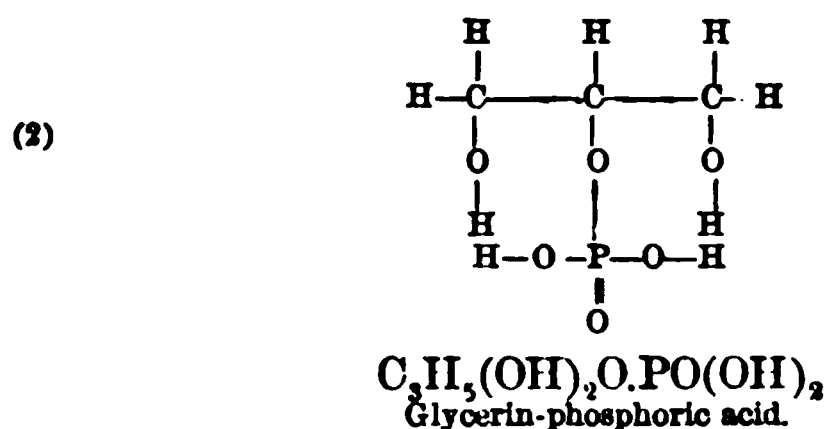
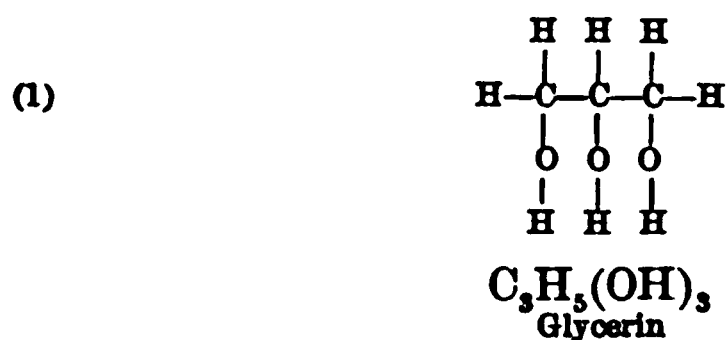
Free glycerin-phosphoric acid is a syrupy fluid possessed of acid taste. Its most characteristic salts are those of barium and calcium. The aqueous solution of the latter is precipitated by heat, the deposit being crystalline (?) Soluble glycerin phosphates are precipitated by lead acetate.

THE LECITHINS.

The brain, the bile, and the ovum in particular, but also other solids and liquids of the animal body, yield a body which has been termed lecithin, or perhaps several bodies, differing only slightly in composition from one another, and which constitute the group of lecithins.

The lecithins are all derived from glycerin-phosphoric acid.

Let us in glycerin-phosphoric acid replace two of the atoms of hydroxyl hydrogen in the glycerin by two molecules of stearyl, and we shall obtain an acid to which the name of distearyl-glycerin-phosphoric acid has been given by Diakonow. The relation of the latter body to glycerin-phosphoric acid is easily seen by comparing their graphic formulæ:—

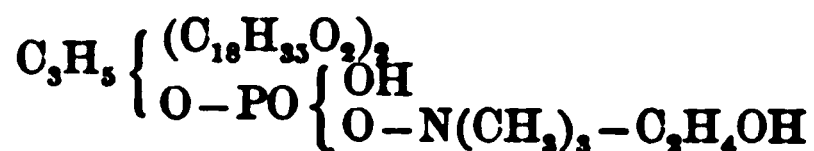


This acid actually occurs as a product of the splitting up of brain-lecithin. It will be apparent to the student that this complex body is a fat and a glycerin-ether.

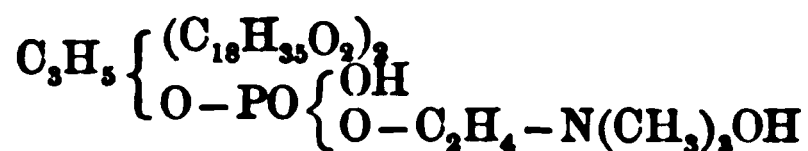
Now this acid can unite itself to a base called neurine, which has the composition $\text{C}_8\text{H}_{18}\text{NO}_2$.

The mode of attachment of neurine to distearyl-glycerin-phosphoric acid cannot be certainly represented by any formula. The three following formulæ for distearyl-lecithin have been suggested and represent the different views which have been held:—

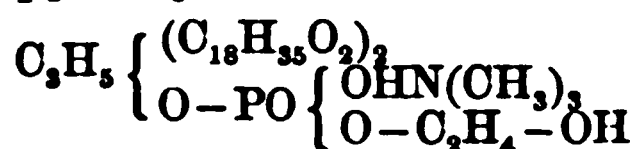
(A.) Diakonow: ¹



(B.) Strecker: ²



(C.) Hoppe-Seyler: ³



Distearyl-lecithin is found in the nerve-centres, and it may be looked upon as the type of the lecithins. We can easily conceive of lecithins which only differ from this one by the radicals of oleic acid or of palmitic acid having taken the place of stearyl. We should thus have dipalmityl-lecithin, or dioleoyl-lecithin formed; such bodies do actually appear to exist.

The lecithins are amorphous, white, bodies which are insoluble in water, little soluble in ether (dipalmityl-lecithin is much more soluble in ether than the others), which readily undergo decomposition at moderate or high temperatures, combining with the elements of water, and yielding as products of decomposition glycerin-phosphoric acid, a fatty acid, and neurine.

Thus distearyl-lecithin when decomposed,



An ethereal solution of lecithin, when shaken with sulphuric acid, is decomposed into distearyl-glycerin-phosphoric acid and neurine, which combines with the acid to form neurine-sulphate.

Any lecithin, if dissolved in alcohol and added to a boiling solution of barium hydrate, is decomposed, phospho-glycerate of barium being formed in every case, and barium stearate, palmitate, or oleate, according to the nature of the lecithin, while neurine remains free.

Alcoholic solutions of lecithin are precipitated by alcoholic solution of platinum tetrachloride.

¹ *Centralblatt f. d. Med. Wiss.* 1868, Nr. 1, s. 8.

² *Ann. Chem. Pharm.* 1868, Bd. cxlviii. s. 77.

³ *Physiological Chem.*, 1877, 1 Theil. s. 80.

Protagon

[Is a glucoside of lecithin (Liebreich), which occurs as the chief proximate constituent of the brain; it is probably also present in those liquids and solids of the body which yield lecithin.]

Unlike lecithin, it can readily and uniformly be crystallized, separating from its solutions in hot alcohol (when these are allowed to cool gradually) in the form of needles, which are usually arranged in tufts or balls. It has approximately the following percentage composition:—C 67·21, H 11·59, N 2·70, P 1·50, O 17·0.

When protagon is boiled with an aqueous solution of barium hydrate, it yields the products of decomposition of lecithin; but, in addition, a nitrogenous body, which appears to be identical with a substance called cerebrin (Müller), to which the formula $C_{17}H_{33}NO_3$ has been ascribed; the latter body is a glucoside, furnishing when boiled with dilute acids considerable quantities of a sweet body which reduces solution of cupric salts, but which is not fermentable.

The existence of protagon has been called in question (Diamkonow, Hoppe-Seyler), it being alleged that protagon is an indefinite mixture of cerebrin and lecithin.]

2. Anhydrides of Sugar.

Certain substances occur very widely diffused throughout the vegetable kingdom which, when subjected to hydrolytic influences, combine with water and form sugar; their close relationship to the sugars, and the fact that, like them, they contain H and O in the proportion in which these elements exist in water, places them amongst the *carbohydrates*, in a group which, after the name of one of its most prominent members, may be termed the group of the amyloses or starches. From their combining with water to form sugar, they may be considered to be anhydrides of sugar. The most characteristic bodies of this group are—

Gum $C_{12}H_{22}O_{11}$
Starch $C_6H_{10}O_5$

Cellulose $C_6H_{10}O_5$
Dextrin $C_6H_{10}O_5$

The formulæ of these bodies, which appear to bear the same relation to the sugars as the ethers bear to the alcohols, are probably multiples of the above, their 'conversion' into sugar being also in reality a process of decomposition.

It appears likely that milk sugar, which, under hydrolytic influences, is changed into a sugar analogous to dextrose—viz. galactose—is an ether of the latter body. Cane-sugar probably bears a somewhat similar relation to dextrose and levulose.

Another class of sugar derivatives exists widely diffused in the

vegetable kingdom, and has some representatives (as chondrin) even in the animal. The term *glucosides* is applied to the members of this group. They appear to be compound ethers of sugars, or of bodies nearly related to them, and under hydrolytic influences they split up into sugar and other atomic groups, many of which possess an aromatic nucleus.

The only anhydride of sugar which occurs in the animal body is—

Glycogen ($C_6H_{10}O_5$)_n, which is a constituent of the liver of all vertebrate animals in a state of health, of the muscles, and of nearly all the organs of the embryo, of the villi of the chorion, and the placental cotyledons. It is also a constituent of many invertebrates, as the mussel (G. Bizio), the tape-worm (M. Foster).

Glycogen is an amorphous, tasteless, white powder, readily soluble in cold water, and quite insoluble in alcohol or ether. Its watery solution always possesses a milky opalescence; it is strongly dextrogyrous. Iodine colours solid glycogen or its watery solution of a brown-red colour.

When boiled with dilute acids, or when subjected to the action of certain animal ferments, as those of the saliva and pancreas, or those contained in the liver, blood, &c., glycogen is easily converted into glucose.

Glycogen is readily obtained from the liver of recently killed animals, and in largest quantities from those of animals which have for some time before death been fed upon starchy or saccharine food, by removing the liver as quickly as possible from the body, plunging it into boiling water, so as to destroy the amyolytic ferment which it contains, and then, having broken up the liver substance, boiling it for some time in water. The milky fluid which is thus obtained contains the glycogen in solution, and from it it can be precipitated by the addition of large quantities of absolute alcohol. For methods of purifying the impure glycogen, the reader is referred to works on physiological chemistry.

5. AMMONIA AND AMMONIACAL DERIVATIVES.

1. *Ammonia* NH_3 , and its salts, the so-called salts of ammonium, occur in traces in many of the constituents of the body, e.g. in the blood.

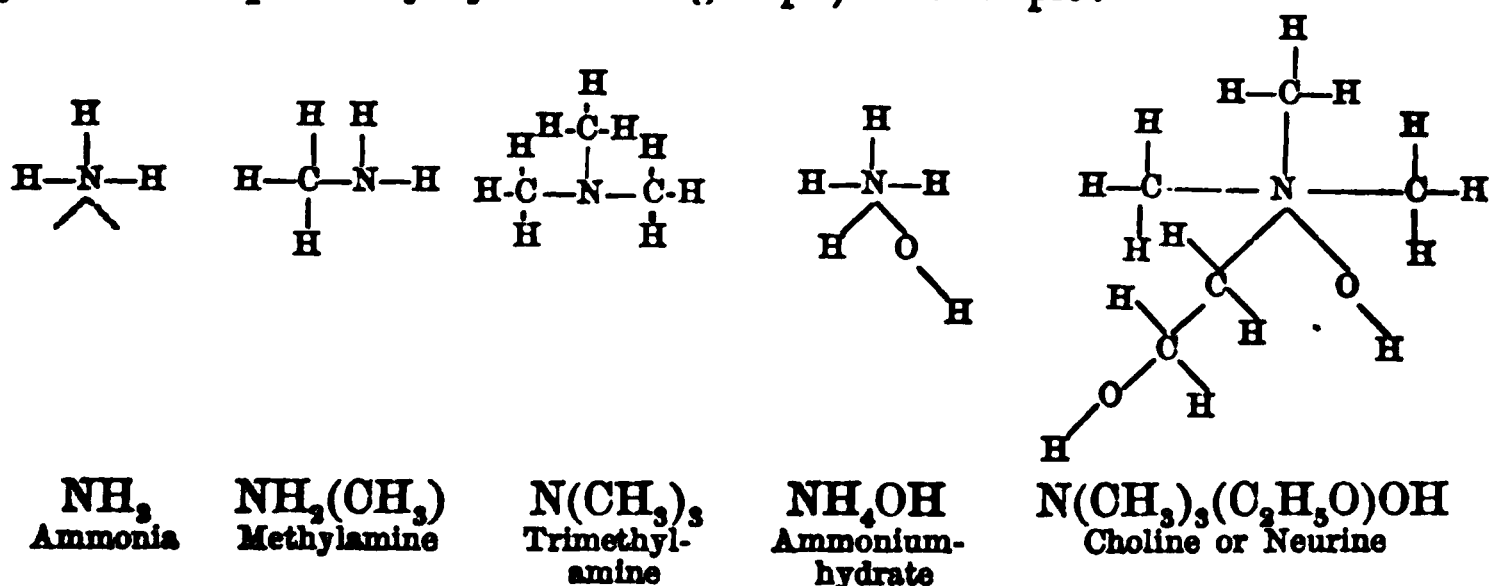
Ammonia can take part in the formation of compounds either by the monatomic group NH_2 , or the diatomic group NH , replacing one or two hydrogen atoms; in other words, the hydrogen atoms in ammonia may be replaced by monatomic or polyatomic molecules.

To the group of ammonia-derivatives belong nearly all the nitrogenous substances of the body, with whose constitution we are well acquainted. These

nitrogenous bodies originate in the albuminous substances and their derivatives, in which bodies the nitrogen is probably present in great part in the form of ammonia, although a portion of it is contained as cyanogen, seeing that some nitrogenous substances contain also cyanogen (*e.g.* uric acid). The following bodies belonging to this class must be mentioned:

a. *Amines*,

which are compounds in which the H-atoms of ammonia or of ammonium-hydrate are replaced by hydrocarbon groups; for example:

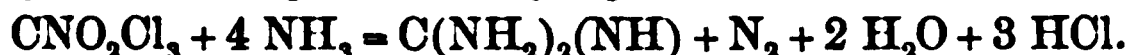


2. Methylamine, $\text{NH}_2(\text{CH}_3)$, and

3. Trimethylamine, $\text{N}(\text{CH}_3)_3$, occur as products of the decomposition of choline and creatine.

4. Choline or neurine, $\text{C}_5\text{H}_{15}\text{NO}_2$, trimethyl-oxyethyl-ammonium-hydrate is one of the products of the decomposition of lecithin. It is obtained synthetically from glyocol and trimethylamine, as may be easily understood by studying the graphic formula of choline; for when we unite the two groups which are joined to the nitrogen by means of the oblique lines, we obtain the graphic formula which represents glyocol, while trimethylamine remains.

5. *Guanidine*, *imido-carbodi-amine*, $\text{C}(\text{NH}_2)_2(\text{NH})$ (or diamido-imido-methane), is a product of the decomposition of guanine $\text{C}_5\text{H}_5\text{N}_5\text{O}$. It is obtained synthetically from chloropicrin $\text{C}(\text{NO}_2)\text{Cl}_3$ and ammonia:



Guanidine is closely related to urea.

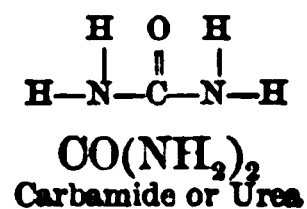
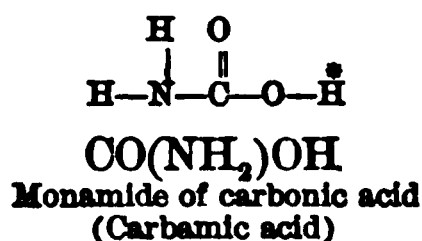
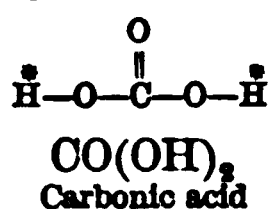
6. *Methyluramine*, methylated guanidine (guanidine in which the group CH_3 has entered, as in the groups of the homologous series of fatty acids), or *diamido-imido-ethane*, $\text{C}_2\text{H}_2(\text{NH}_2)_2(\text{NH})$, is a product of the decomposition of creatine.

b. *Amides*

are compounds in which the OH-group in acids is replaced by NH_2 .

7. *Urea or Carbamide* $\text{CO}(\text{NH}_2)_2$.—In the molecule of carbonic acid $\text{CO}(\text{OH})_2$ we may replace either one or both hydroxyls by NH_2 ; in the first case we give rise to the monamide carbamic acid, in the second case to the diamide known as carbamide or urea. The first has only lately been recognised as a constituent of the animal organism, whilst the latter is the chief product of the retrograde metamorphosis of its nitrogenous constituents.

The relations of carbonic acid, carbamic acid, and urea are seen by referring to the appended graphic formulæ :



It has been asserted by Drechsel that carbamic acid exists in the blood (*Sitzungsberichte d. k. sächs. Acad. der Wissenschaften*. Math.-Phys. Kl. 1875), but the fact has been denied by Hofmeister (*Pflüger's Archiv*, 1876, S 337-347), though on insufficient grounds.

Urea is the chief and most characteristic constituent of the urine of man and of carnivorous mammals, and is also found in the urine of the herbivora, of birds, and of many reptiles. It is a normal though very scanty constituent of the blood, and of fluids which transude from it, and is constantly found in the liver.

Urea can readily be obtained from human urine by concentrating it, decanting the dark-coloured fluid from the deposit of insoluble salts formed during the process of evaporation, and adding strong and pure nitric acid, when a crystalline mass of nitrate of urea ($\text{CH}_4\text{N}_2\text{O}, \text{HNO}_3$) separates; this is pressed, washed with a little ice-cold water, then dissolved in boiling water, to which is added an excess of barium carbonate and pure animal charcoal. On evaporating to dryness and boiling the residue with alcohol, urea is dissolved, and may be obtained on evaporating the fluid and allowing it to crystallize.

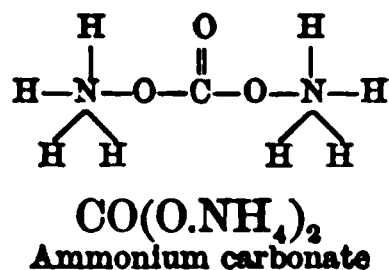
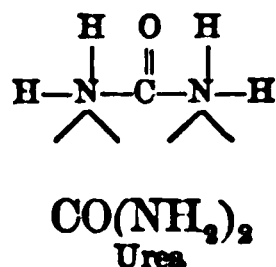
Urea crystallizes in colourless needles or in long four-sided prisms, which belong to the rhombic system.

Urea is inodorous; it possesses a cooling and somewhat bitter taste, not unlike that of nitre, and is very readily soluble in water and alcohol. The following reactions of urea are of special importance :

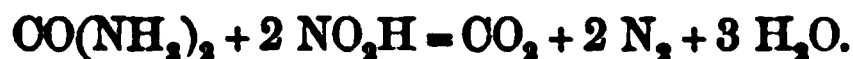
a. In the presence of decomposing animal substances (specially when its solutions are mixed with decomposing urine), when boiled with alkalies, or when superheated with water, urea combines with $2 \text{H}_2\text{O}$, and is converted into ammonium carbonate; thus :



The relations of urea to ammonium carbonate are shown below :



b. When treated with nitrous acid, urea is at once decomposed, as follows :



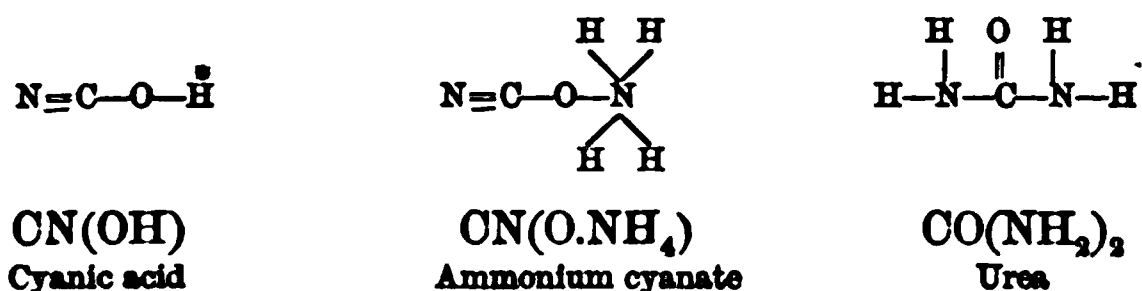
c. When treated with solutions of alkaline hypobromites, solutions of urea are decomposed into carbonic acid and nitrogen, the former being absorbed by the alkaline hypobromite.

d. Mercuric nitrate produces in solutions of urea a white precipitate having the composition $2 (\text{CO}(\text{NH}_2)_2) + 3 \text{HgO} + \text{Hg}(\text{NO}_3)_2$.

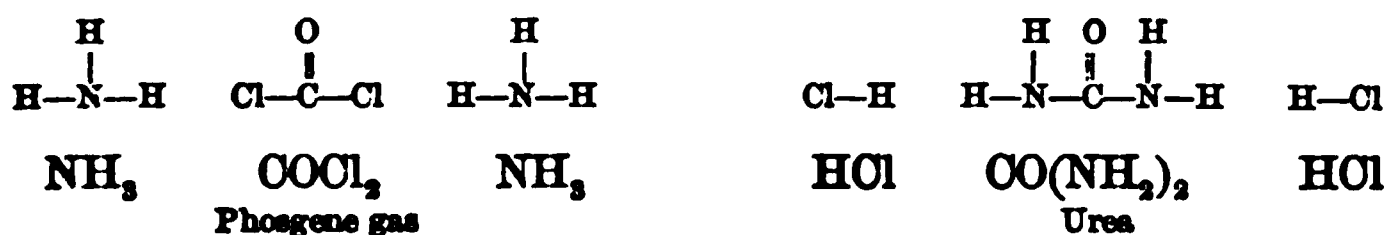
Upon this reaction is based Liebig's method of determining urea in urine. Two volumes of urine are mixed with one volume of so-called *baryta-mixture* (which is made by mixing equal volumes of concentrated solution of barium hydrate and cold saturated solution of barium nitrate), with the object of precipitating the phosphates and sulphates contained in the urine.

To 15 C.C. of the filtrate, corresponding to 10 C.C. of urine, a solution of mercuric nitrate of known strength is added as long as a precipitate is formed. The end of the reaction is ascertained by adding a solution of sodium carbonate to a drop of the liquid; a yellow precipitate forms as soon as more mercury solution has been added than is required to combine with the urea. The mercury solution is usually of such strength that 1 C.C. corresponds to 0.01 gm. of urea.

Synthesis of Urea, and its relations to other bodies.—Urea was the first organic substance which was synthetically obtained (Wöhler); it can be made artificially by many processes, as by heating ammonium cyanate, when a rearrangement of atoms takes place ($\text{ON}(\text{O.NH}_2) = \text{CO}(\text{NH}_2)_2$).



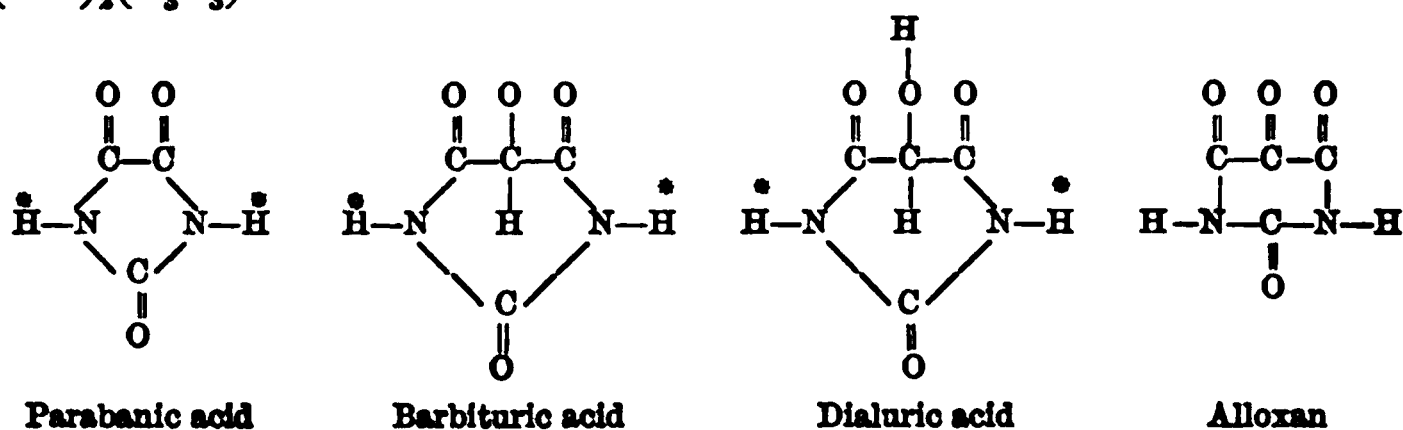
Urea can also be prepared from carbonyl chloride (phosgene gas) and ammonia :



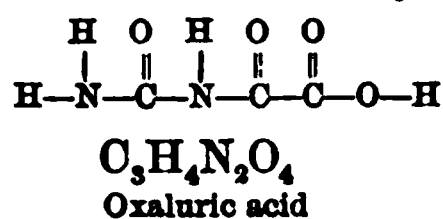
Urea differs from guanidine in that in the latter body the carbon atom is joined to the diatomic molecule NH , instead of to an O -atom.

In both the NH_2 -molecules of urea, the H -atoms admit of being replaced by alcohol- or acid-radicals. Combinations of the latter kind—namely, where 2 H , are replaced by diatomic acid radicals—are often obtained, in addition to ordinary urea, in the artificial oxidation of uric acid (which is itself a body of the same kind, only more complex). The radicals of the oxalic acid series and their immediate derivatives are, indeed, such compound ureas; some of them are called acids, for the last H -atom of the amide group, which is still present, can be replaced by a metal. Some of these bodies are: Parabanic acid (oxalyl-urea) $\text{CO}(\text{NH})_2(\text{C}_2\text{O}_2)$, Barbituric acid (malonyl-urea) $\text{CO}(\text{NH})_2(\text{C}_2\text{H}_2\text{O}_3)$,

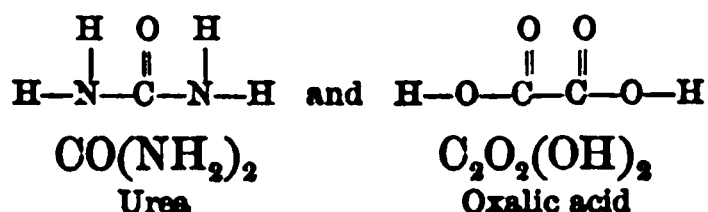
Dialuric acid (tartronyl-urea) $\text{CO}(\text{NH})_2(\text{C}_3\text{H}_2\text{O}_3)$, Alloxan (mesoxalylic-urea) $\text{CO}(\text{NH})_2(\text{C}_3\text{O}_3)$.



When subjected to hydrolytic processes these ureas combine with one or two molecules of H_2O ; in the first case the ring as it were opens, and an acid is formed in which only one of the OH groups is replaced by urea; if two molecules, however, enter, urea entirely separates from the acid; *e.g.*, in the case of parabanic acid, the first molecule of water yields oxaluric acid.



The second molecule of water leads to the formation of



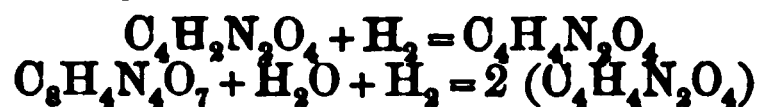
When reduced, alloxan furnishes alloxantin ($\text{C}_8\text{H}_4\text{N}_4\text{O}_7$).



Alloxantin is an ether-like combination of alloxan and dialuric acid (see above), and on the addition of H_2O yields these two substances:

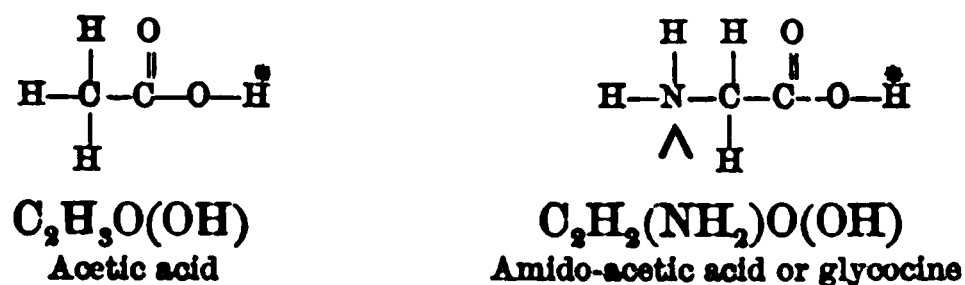


Dialuric acid is obtained by the further reduction of alloxan or alloxantin:

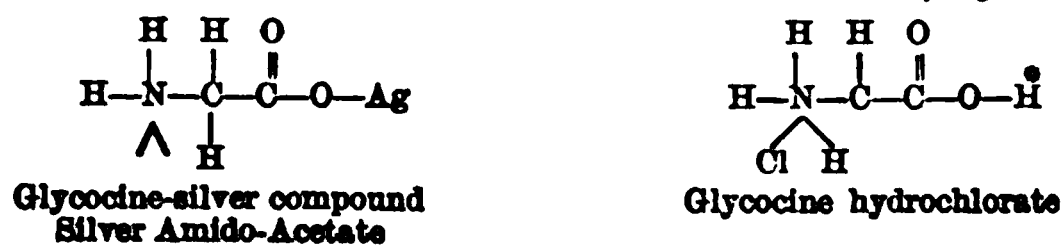


c. Amido-Acids

are acids in which hydrogen atoms of the acid radical are replaced by NH_2 ; for instance:

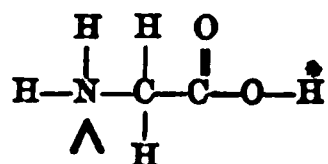


The amido-acids behave, on the one hand, as acids, on the other as bases, inasmuch as their ammoniacal residue combines with acids, *e.g.*



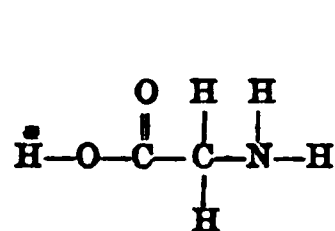
When treated with nitrous acid the amido-acids yield oxy-acids; thus the amido-fatty acids yield the oxy-fatty acids (Glycollic Acids, p. 14), by the replacement of the molecule NH_2 by the molecule OH .

8. *Glycocine* (glycocol, sugar of gelatin, amido-acetic acid), $\text{C}_2\text{H}_5(\text{NH}_2)\text{O.OH}$, does not occur, as such, in the body, but forms part of so-called conjugate acids, and exists in complex combinations in gelatin.

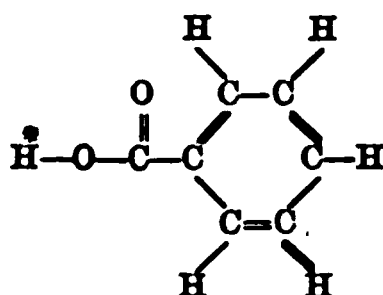


$\text{C}_2\text{H}_5(\text{NH}_2)\text{O(OH)}$
Amido-acetic acid or glycocine

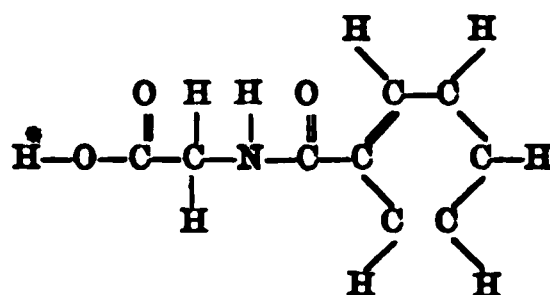
Glycocine when treated with nitrous acid yields oxy-acetic or glycollic acid. It can be prepared synthetically from chloracetic acid and ammonia. It unites with monobasic acids so as to form compounds, in which one H-atom of the NH_2 is replaced by the acid radical (the OH-group and the H-atom combining to form H_2O), thus:



Glycococine



Benzoic acid



Hippuric acid

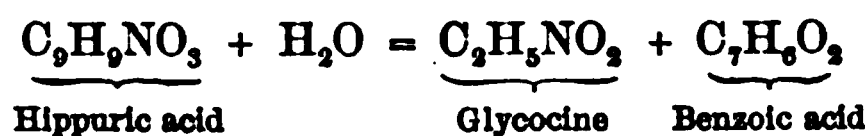


The following are compounds which under hydrolytic influences combine with H_2O and split up into glycocine and an acid: they are called conjugate acids:

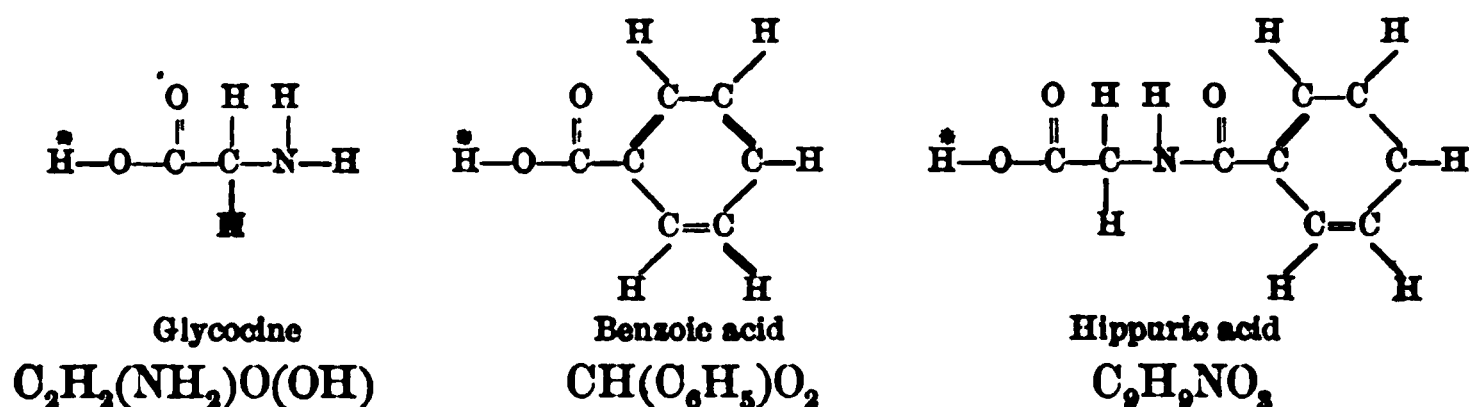
Glycocholic acid (see p. 18) $\text{C}_{26}\text{H}_{43}\text{NO}_6$ is a constituent of the bile.

Hippuric (Benzamidacetic) acid $\text{C}_9\text{H}_9\text{NO}_3$ occurs in small quantities as a constant constituent of the urine of man, and in large quantities in the urine of herbivorous animals; it is, indeed, the chief nitrogenous proximate principle contained in the urine of the latter. Hippuric acid occurs besides in the urine of all animals, if benzoic or some other aromatic acids—such as cinnamic, mandelic, or chnic acid—form a part of their food.

When hippuric acid is boiled with hydrochloric acid for some time, it combines with the elements of water and yields glycocine and benzoic acid; thus—



The relation which these two products bear to hippuric acid is rendered more plain by a study of the appended graphic formulæ:



Knowing these relations of hippuric acid, it is not difficult to conceive that after benzoic acid has been introduced into the organism, hippuric acid should be excreted; we have only to conceive that in its passage through the organism it should encounter glycocine, a body which we already know as occurring in the conjugated bile acids, and then it is easy to understand that this compound acid should arise.

Whence, however, is the hippuric acid derived which is excreted in such large quantities in the urine of the herbivora? This is a question which must be looked upon as yet undecided. In all probability the aromatic nucleus of hippuric acid is derived from some non-nitrogenous body existing in the food of the herbivora, which can readily undergo conversion into benzoic acid.

Such a body is probably chinic acid $\text{C}_7\text{H}_{12}\text{O}_6$, or a body closely related to it (perhaps $\text{C}_7\text{H}_6\text{O}_5$). Whilst the researches of the chemist tell us that this acid yields, when it is reduced, benzoic acid, physiological experiments have shown that, after the injection of a salt of chinic acid, hippuric acid is excreted.

Hippuric acid when pure occurs in the form of slender four-sided, hard, somewhat opaque prisms belonging to the rhombic system. It requires for solution 600 parts of cold water, but it is much more readily soluble in hot water than alcohol. Its solutions have a strong acid reaction.

When heated in a narrow glass tube, hippuric acid is observed first of all to melt, and on cooling the product a crystalline mass is obtained; when heated more strongly, it yields a crystalline sublimate of benzoic acid, ammonium benzoate, and oily drops; when heated more strongly, it yields cyanogen compounds.

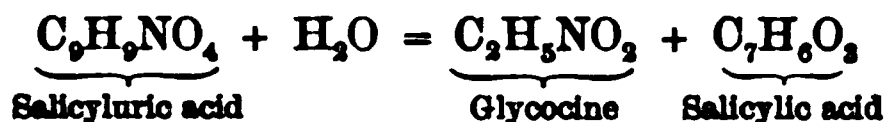
When boiled with nitric acid and the acid driven off by evaporation, the residue smells of nitrobenzol, and the colour reactions of this body may be obtained.

Hippuric acid is a monobasic acid; its silver salt is soluble in hot water, and is deposited in crystalline needles from it on cooling.

Hippuric acid can be readily obtained in an impure condition from the urine of the cow or of the horse by boiling it with milk of lime for some time, filtering, concentrating the filtrate until its bulk is one-sixth or one-eighth that of the original urine, and then

adding hydrochloric acid. Hippuric acid separates in the form of a highly-coloured crystalline mass. This may be purified by solution and decolorization with animal charcoal.

Other aromatic acids possess the power, like benzoic acid, of linking themselves to glycocine in the system, and of forming compounds analogous to hippuric acid. Thus, after salicylic acid $C_7H_6O_3$ has been introduced into the body, salicyluric acid $C_9H_9NO_4$ is excreted in the urine. The latter acid readily decomposes into glycocine and salicylic acid; thus—



Similarly, in passing through the system, anisic (formobenzoic acid) is converted into anisuric acid, and toluic into toluric acid.

9. *Alanine*, amido-propionic acid, $C_3H_7(NH_2)O.OH$, does not occur in the animal body.

10. *Butalanine*, amido-valerianic acid, $C_5H_9(NH_2)O.OH$, is said to accompany leucine in some animal tissues.

11. *Leucine*, or amidocaproic acid, $C_6H_{11}(NH_2)O.OH$, occurs as a constituent of many glandular organs, and especially of the pancreas. It is a constituent of the urine in certain diseases, especially in acute yellow atrophy of the liver, and is one of the products of the decomposition of the proteids by the pancreatic proteolytic ferment, being, however, also produced during the putrefactive decomposition of the proteids and by the action of strong acids and alkalies upon them.

Leucine is soluble in 27 parts of cold water; it is very sparingly soluble in cold and hot alcohol. It crystallises from its solution in nodules and balls, which sometimes exhibit radiating markings, and which occasionally are formed of radially arranged plates.

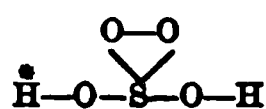
Leucine melts at 170° and may be sublimed.

12. *Serine* is probably amidolactic acid $C_3H_5(NH_2)O_2$, and is obtained, in addition to leucine and tyrosine, when silk-gelatine is boiled with acids.

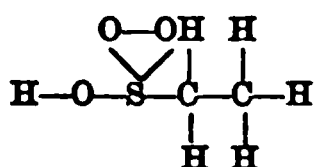
When treated with nitrous acid it yields oxylactic acid or glyceric acid.

13. *Cystine* $C_3H_7NSO_2$ has been considered as serine, in which one atom of oxygen has been replaced by S, and as having probably the same constitution. It is a constituent of the kidneys, and is occasionally found in the urine and in urinary calculi. The formula of cystine is probably $C_3H_7NSO_2$; when decomposed by means of nitrous acid it does *not* yield glyceric acid, as would almost certainly be the case if it were derived from serine (Dewar and Gamgee).

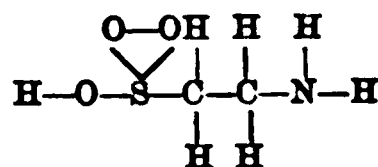
14. *Taurine*, amido-ethyl-sulphonic acid, $\text{SO}_2(\text{OH})(\text{C}_2\text{H}_4\cdot\text{H}_2\text{N})$



$\text{SO}_2(\text{OH})_2$
Sulphuric acid



$\text{SO}_2(\text{OH})(\text{C}_2\text{H}_5)$
Ethylsulphonic acid



$\text{SO}_2(\text{OH})(\text{C}_2\text{H}_4\cdot\text{H}_2\text{N})$
Amido-ethyl-sulphonic acid or Taurine

This body occurs in the bile as a compound of cholic acid, similar to that of glycocine, viz. as *Taurocholic acid* ($\text{C}_{26}\text{H}_{45}\text{NSO}_7$); it is also present in a free condition in some glands.

15. *Tyrosine*, $\text{C}_9\text{H}_{11}\text{NO}_3$, is an amido-acid, whose constitution is not yet known, but which contains as its basis an aromatic residue; it is generally found in small quantities accompanying leucine. Like leucine, it is an ingredient of glandular organs, and is a product of the digestion and decomposition of proteids; it also occurs in the urine in cases of acute yellow atrophy.

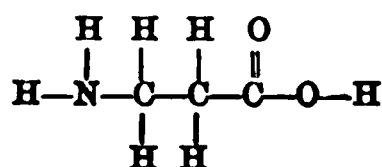
When heated with mercuric nitrate, in presence of some nitrous acid, tyrosine yields a red coloration.

d. Amido acids, in which the hydrogen of the ammoniacal residue is itself substituted.

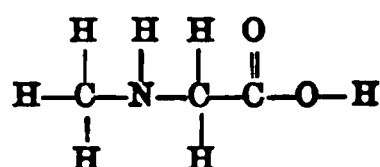
16. *Sarcosine*, methyl-amido-acetic acid or methyl-glycocine,



is obtained when creatine is treated with alkalis, or synthetically by the action of methylamine on chloracetic acid (refer to p. 39 for the synthesis of Glycocine). It is an isomer of alanine.

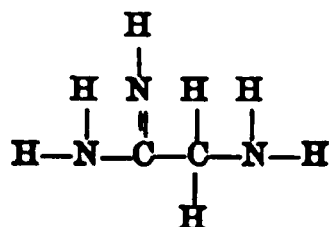


$\text{C}_3\text{H}_7\text{NO}_2$
Alanine

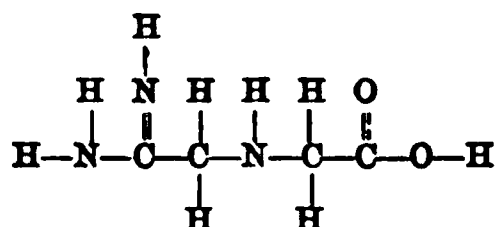


$\text{C}_3\text{H}_7\text{NO}_2$
Sarcosine

17. *Creatine*, methyl-guanidine-acetic acid, $\text{C}_4\text{H}_9\text{N}_3\text{O}_2$, is a constituent of the blood, the muscles, the brain, &c.

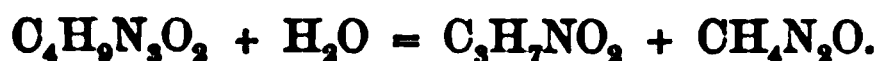


Methyl-guanidine

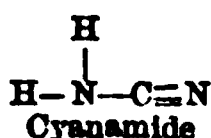


Methyl-guanidine-acetic acid (Creatine)

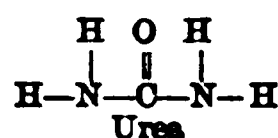
Creatine is obtained synthetically from cyanamide (CN.NH_2), and sarcosine; one can in the graphic formula of creatine easily recognise, on the left, the residue of cyanamide, and, on the right, that of urea.



Actually, urea only differs from cyanamide in containing one molecule more of H_2O .



Cyanamide



Urea

When oxidized (by means of mercuric oxide, peroxide of lead, &c.), creatine yields methyl-guanidine and oxalic acid, a decomposition which is intelligible enough when we consider that both methyl-guanidine and acetic acid occur in creatine, and that oxalic acid is a doubly oxidized acetic acid (p. 16).

By other methods of oxidation, creatine yields methyl-parabanic acid, which is also an intelligible enough reaction.

c. Ammoniacal Derivatives of unknown Constitution.

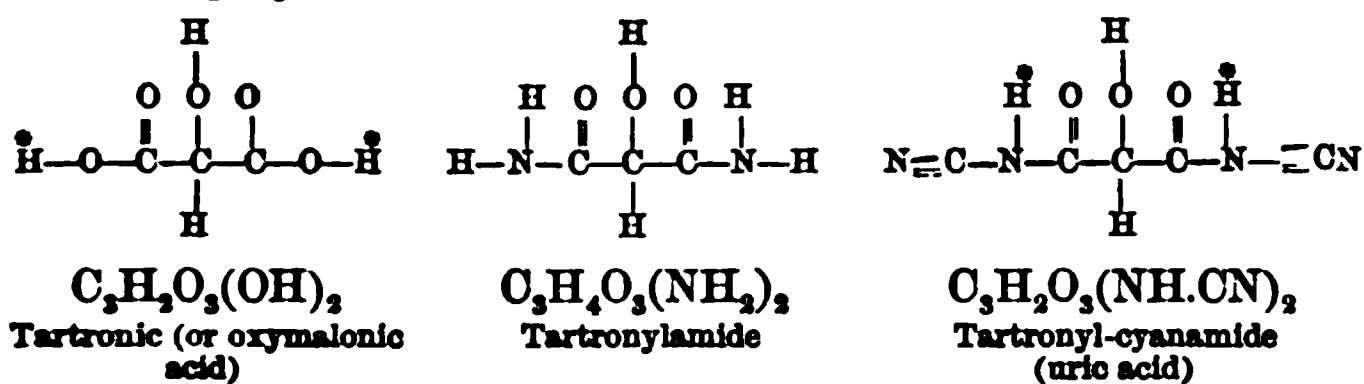
18. *Uric acid* $C_5H_4N_4O_3$ is a constituent of the urine of man and the carnivora, and is found in smaller quantities in that of the herbivora. In some classes of animals it constitutes the chief urinary constituent.

Uric acid, when pure, presents the appearance of a white powder which consists of minute microscopic crystals. It is inodorous and tasteless; it is insoluble in cold water, requiring 14,000 parts to dissolve it, and is very sparingly soluble in hot water. It is insoluble in alcohol or ether.

It is readily obtained, though somewhat contaminated with colouring matter, by acidulating urine with hydrochloric or nitric acid, and allowing it to stand for 24 or 36 hours. By dissolving the coloured crystals thus obtained in a solution of sodium or potassium hydrate, and then neutralizing with an acid, colourless uric acid may be obtained.

Murexide test. When treated with nitric acid and evaporated to dryness, uric acid yields a golden-red residue, which is coloured purple-red (murexide, purpurate of ammonia) by ammonia, and blue by potash.

The most probable view of the constitution of uric acid is that it is *tartronylcyanamide*.



Uric acid is bibasic, as in it, as in compound ureas (p. 38), both the remaining H-atoms of the amide groups are replaceable by metals. Of the salts, of which the acid ones are, like uric acid itself, very slightly soluble in water, those of sodium and ammonium occur in man, chiefly in pathological conditions.

By oxidation, uric acid yields:

a, in presence of acids, alloxan and urea:



(Alloxan yields on further oxidation carbonic acid and parabanic acid, $C_4N_2H_2O_4 + O = CO_2 + C_3H_2N_2O_3$).

b, in presence of alkalies, allantoinine ($C_4H_6N_4O_3$) and carbonic acid:



19. *Xanthine* $C_5H_4N_4O_3$ occurs in traces in many organs of the body and in the urine, and can artificially be obtained from hypoxanthine. A body isomeric with it is obtained from guanine.

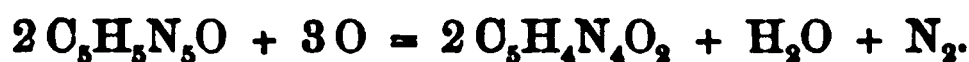
20. *Hypoxanthine*, or *Sarcine*, $C_5H_4N_4O$, occurs together with xanthine, into which it is converted by the action of oxidizing agents.

21. *Carnine* $C_7H_8N_4O_3$ occurs in small quantities in extract of meat (Weidel); under the influence of bromine it is oxidized to hypoxanthine:

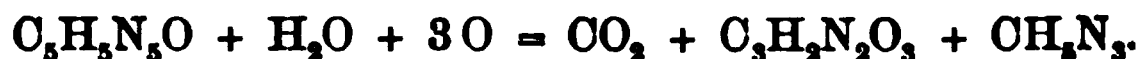


22. *Guanine* $C_5H_5N_5O$ occurs in small quantities in the pancreas and liver, as well as in guano and the excrements of spiders.

When oxidized, guanine yields a body which is isomeric with xanthine (isoxanthine), nitrogen being evolved,

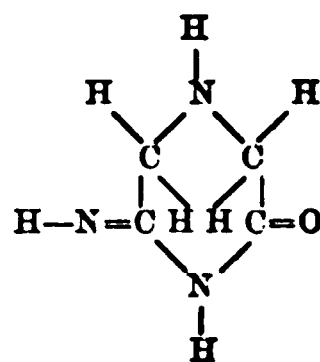
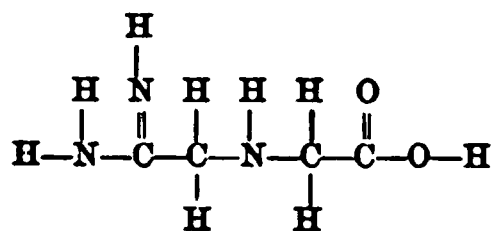


Other oxidizing agents split it up into carbonic acid, parabanic acid and guanidine,



23. *Creatinine* $C_4H_7N_3O$ is a constituent of urine.

Creatinine is a strongly alkaline substance; it forms a characteristic crystalline compound with chlorine of zinc. It is an anhydride of creatine, from which it is easily obtained, and into which it is easily reconverted. The most probable view of the formation of this anhydride is shown in the accompanying formula:—



24. *Inosinic acid* $C_5H_8N_2O_6$, a constituent of muscles.

25. *Kynurenic acid* $C_{20}H_{14}N_2O_6$ occurs in the urine of dogs.

26. *Allantoinine* $C_4H_6N_4O_3$ is a constituent of the urine of the foetus and the sucking infant. It is obtained by the oxidation of uric acid. Under hydrolytic influences allantoinine splits into urea and allanturic acid ($C_3H_4N_2O_3$); thus



27. *The Colouring Matters of the Animal Body.*

These substances, of which the best known are connected with the derivatives of ammonia, are in general crystallizable, and probably originate in, or are derived from, one substance which contains iron and is called hæmatin. As our knowledge of the constitution and chemical relations of the animal-colouring matters is comparatively slight, it is most convenient to classify them, according to the fluids of the body in which they occur, into

- a*, Colouring matter of the blood and its derivatives.
- b*, Colouring matters of the bile and their derivatives.
- c*, Colouring matters occurring in the urine and their derivatives.
- d*, Melanin and other sparsely diffused colouring matters.

a. In the case of the blood-colouring matter hæmoglobin, it is expedient to postpone a full account of its compounds, properties and derivatives to the chapter in which the physiology of the blood is treated of; for it affords an instance in which the chemical and physical properties of a proximate principle offer the most complete explanation of its function in the body. In order, however, to enable the reader to appreciate some of the remarks which have to be made in reference to the bile-colouring matters, a few words may be said in this place.

Hæmoglobin is a red colouring matter contained in the red-blood corpuscles which can be obtained from the blood of most animals in a crystalline condition. It has approximately the following percentage composition—C 54·0, H 7·25, N 16·25, S 0·63, Fe 0·42, O 21·45. If we assume that its molecule contains one atom of iron, hæmoglobin will have the formula $C_{600}H_{960}N_{154}FeS_3O_{177}$.

Under various circumstances this complex body splits up into an albuminous body and into hæmatin $C_{34}H_{34}N_4FeO_5$ or $C_{69}H_{70}N_8Fe_2O_{10}$ (Hoppe-Seyler), the latter containing all the iron of the hæmoglobin from which it is derived. Hæmatin contains between 8·78 and 8·88 per cent. of Fe; it forms a crystalline hydrochlorate called hæmin.

b. Colouring matters of the bile.

Bilirubin ($C_{16}H_{18}N_2O_3$ Städeler).—This body, which has been described under the name of cholepyrrhin and biliphaein, appears to be the normal colouring matter of the bile of man and of carnivorous animals generally. It is a frequent constituent of biliary calculi, in which it occurs combined with lime, and in small

quantities it occurs in old sanguineous extravasations. The latter fact argues very strongly in favour of the view, which receives support from other considerations, that bilirubin is derived from the hæmatin of hæmoglobin.

Bilirubin occurs both in an amorphous and in a crystalline condition. Its colour is orange red; it is insoluble in water, very slightly soluble in ether, somewhat more soluble in alcohol, but much more soluble in chloroform. All solutions of bilirubin exhibit, even when highly diluted, a yellow colour.

Bilirubin is soluble in alkaline solutions, from which it is precipitated on neutralization with acids.

Bilirubin forms compounds with bases, playing the part of a monobasic acid. Its calcium compound has the composition $C_{16}H_{17}CaN_2O_3$; it is insoluble in water, alcohol, ether, and chloroform. It is, however, easily decomposed by means of hydrochloric acid, and then the liberated bilirubin can be extracted by chloroform.

When subjected to oxidizing agents, bilirubin is converted into *biliverdin*, and afterwards into bilicyanin and choletelin.

Preparation of bilirubin.—Bilirubin is best prepared from the gall-stones of the ox, which are richer in this substance than those of man, and in which it is not, as in the latter, mixed with cholesterin.

The gall-stones are dried, powdered, and extracted successively with boiling water, boiling ether, and then with successive quantities of dilute hydrochloric acid; the residue is dried and treated with repeated quantities of chloroform; these chloroform solutions are mixed, and the greater part of the chloroform is distilled off. On adding alcohol the bilirubin is precipitated as an amorphous orange-yellow powder very similar to antimony sulphide.

Gmelin's reaction.—When a solution of bilirubin, or the dry substance itself, is treated with nitric acid which is coloured with nitrous acid, a play of colour is produced, blue, violet, and green alternating, giving place finally to a dirty claret colour.

Biliverdin ($C_{16}H_{20}N_2O_5$ Städeler; $C_{16}H_{18}N_2O_4$ Maly).—This colouring matter does not appear to occur in the human organism; it is, however, found at the edges of the placenta in the dog, and it occurs occasionally even in man in vomited matters, in the alvine dejections, and, it is said, sometimes in the urine.

Bilirubin in solution is, on exposure to the air, converted into biliverdin, the process being hastened by alkalinity of the fluid. Thus, if bilirubin be dissolved in dilute solution of sodium hydrate and exposed to the air, the solution generally becomes green; and then, on adding hydrochloric acid, biliverdin is precipitated. Biliverdin may also conveniently be prepared by digesting pure bilirubin for a couple of days in monochloroacetic acid at a gentle temperature. The simple addition of water is sufficient to precipitate the biliverdin (Maly, 'Untersuchungen über die Gallenfarbstoffe,' IV. *Abhandlung. Sitzungsberichte d. Wiener Akademie* 70, III. Abtheil. 1874).

Biliverdin is an amorphous dark-green body, insoluble in water, ether, and

chloroform, but very soluble in alcohol, the solution having a beautiful green colour. Biliverdin is readily soluble in alkaline solutions.

Bilifuscin $C_{16}H_{20}N_2O_4$ (= bilirubin + H_2O) is a black shining amorphous body, insoluble in water, ether, and chloroform, but readily soluble in alcohol, which it colours brown; it is contained in small quantities in the gall-stones of man.

Biliprasin $C_{16}H_{22}N_2O_6$ (= bilifuscin + H_2O + O) is present in small quantities in some human gall-stones.

Bilicyanin (Heynsius and Campbell, 'Die Oxydations-producte der Gallenfarbstoffe und ihre Absorptionstreifen,' *Pflüger's Archiv*. 1871, p. 461) is the name which has been applied to an imperfectly studied and yet not separated body which is produced during the oxidation of bilirubin, and which appears to be intermediate between bilirubin and biliverdin. This is the same body which has been described by Stokvis under the name of cholecyanin ('Das Gmelin'sche (blaue) Oxidations product der Gallenfarbstoffe,' *Centralblatt f. d. med. Wissenschaft*, 1872, No. 50).

Choleletin is an imperfectly studied oxidation-product obtained from bilirubin by acting upon it with nitrous acid (Maly). By Stokvis, as well as by Heynsius and Campbell, choleletin has been considered to be identical with hydrobilirubin. The spectroscopic researches of Vierordt, however, establish a difference (Vierordt, 'Physiologische Spektralanalyz,' *Zeitschrift f. Biologie*, 1874, 10, 399-409).

Hydrobilirubin.—When bilirubin is dissolved in a dilute solution of sodium or potassium hydrate, and subjected to the action of sodium amalgam for some days, the dark opaque solution becomes transparent and of a golden-yellow colour, and hydrochloric acid then throws down from it, in the form of brown-red flakes, a pigment which resembles bilirubin in its capability of uniting itself in bases. This pigment is easily soluble in alcohol, slightly soluble in water, and is readily dissolved by alkaline fluids. Such alkaline solutions possess the colour of urine.

The spectroscopic characters of this solution are very marked. Acid solutions exhibit a sharply-defined absorption band between the green and blue corresponding to the space between Fraunhofer's lines b—F. In alkaline solutions this band is fainter. On the addition of a few drops of solution of zinc chloride to the fluid, the latter assumes a rose-red colouration and a green fluorescence, the absorption band becoming more deeply marked. To this body Maly¹ has ascribed the formula $C_{32}H_{40}N_4O_7$; but, as Heynsius has remarked, very little importance can be attached to such a formula obtained by the analysis of a probably impure product.

Hydrobilirubin is believed to be identical with a colouring matter found in the alcoholic extract of intestinal contents by Vanlair and Masius,² and called by them Sterco-bilin; and it is looked upon generally as identical with the body to be afterwards

¹ Richard Maly (1) 'Künstliche Umwandlung von Bilirubin in Harnfarbstoff,' *Centralblatt f. d. med. Wissenschaft*, 1871, No. 54; (2) 'Umwandlung von Bilirubin in Harnfarbstoff,' *Annal. d. Chem.* 163, pp. 77-95.

² Vanlair and Masius, *Centralblatt f. d. med. Wissenschaft*, 1871, No. 24.

referred to as Urobilin, which was discovered by Jaffe as a frequent constituent of the urine.¹ From the researches of Hoppe-Seyler it would appear² that a body which he obtained by reducing an alcoholic solution of hæmatin by means of tin and hydrochloric acid, or by the action of these reagents on hæmoglobin, is identical with hydrobilirubin.

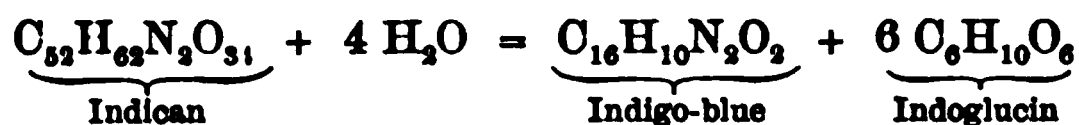
c. Colouring matters of the urine.

These appear to be three in number, viz. :

1. Urochrome.—This is, according to Thudichum, the normal colouring matter, in virtue of which urine possesses its peculiar amber colour. In order to obtain it, 'fresh urine is treated with excess of milk of lime or baryta, and allowed to stand on filtered. To the filtrate lead acetate, with a little ammonia, is added till colourless, and the precipitate well washed and digested with cold dilute sulphuric acid till a filtered sample shows an excess of sulphuric acid when treated with barium chloride and hydrochloric acid. At this point filter the whole, shake the filtrate with barium carbonate to remove the sulphuric acid, add a little baryta water, pass carbonic acid through the liquid, and filter again. Precipitate the solution with mercuric acetate, wash the precipitate of urochrome mercury very thoroughly with cold and hot water, decompose it by sulphuretted hydrogen, filter, shake the filtrate with a little pure silver oxide to remove hydrochloric ~~or~~ kryptophanic acid, filter; again decompose by sulphuretted hydrogen, and evaporate the filtrate to dryness in vacuo over sulphuric acid. A yellow uncrystallizable mass of urochrome remains.'³

Urochrome is said to be easily soluble in water, colouring it yellow, and very little soluble in alcohol; its aqueous solution becomes red on standing, depositing resinous flakes.

2. Indican $C_{52}H_{62}N_2O_{31}$.—Normal urine appears to contain as a constant constituent small quantities of indican. This body is a glucoside which, when boiled with acids or subjected to certain fermentation processes, splits up into a peculiar sugar (indoglucin) $C_6H_{10}O_6$, and into indigotin or indigo-blue $C_{16}H_{10}N_2O_2$; thus—



Indican can be obtained in a somewhat impure condition from urine by precipitating the fluid with lead acetate and adding ammonia to the filtrate. The precipitate thrown down by ammonia is suspended in alcohol, decomposed by sulphuretted hydrogen,

¹ Jaffe, *Virchow's Archiv*, Bd. 47, 405; *Centralblatt f. d. med. Wissenschaft*, 1871, No. 54.

² Hoppe-Seyler, 'Einfache Darstellung von Harnfarbstoff (Hydrobilirubin) aus Blutfarbstoff,' *Bericht d. D. Chem. Gesellschaft*, 1065–1066.

³ Thudichum, *Chemical Physiology*, pp. 186, 187.

and the alcoholic solution separated from the precipitated lead sulphide yields, on evaporation, a yellow syrupy fluid containing impure indican.

Indican is recognized as a constituent of urine chiefly by the fact that when this fluid is allowed to decompose indigo-blue is frequently observed to be deposited, and also by the production of indigo-blue when urine is boiled with hydrochloric acid.

It has been observed that the subcutaneous injection of indol, $C_{10}H_{14}N_2$, leads to the excretion of indican; and the same result follows the injection of salicylic acid.

3. Urobilin.—This body, which appears to be identical with hydrobilirubin, is not a constant constituent, but has been frequently observed in the urine in fevers.

d. Melanin and allied pigments.

Amongst the more sparingly diffused and least known of the colouring matters of the body are certain brown and black pigments which occur in the cells of the choroid, in those of the rete malpighii of the skin—especially of the dark races—in the bronchial glands, and in some morbid growths. These black and brown pigments all contain C, H, O, N, but in no constant proportions; they are insoluble in water, alcohol, and ether, but are in part dissolved by boiling in solutions of the caustic alkalies.

These bodies are probably related to hæmatin, though no certain information is possessed on this matter.

6. BODIES OF UNKNOWN CONSTITUTION.

A. The Proteids.

The bodies included in this category are highly complex non-crystallisable compounds of carbon, hydrogen, oxygen, nitrogen and sulphur, occurring in a solid viscous condition, or in solution in nearly all the solids and fluids of the organism. The different members of this group present differences in physical and, to a certain extent, even in chemical properties; they all possess, however, certain common chemical reactions, and are united by a close genetic relationship.

The proteids of the animal body are all derived, directly or indirectly, from vegetable organisms, which possess the power of constructing them from the comparatively simple substances which form their food. Such a synthesis never takes place in the animal body, though the latter possesses the power of converting any vegetable or animal proteid into the various proteids which are characteristic of its solids and liquids.

All the proteid substances which enter the animal body are, by the influence of certain ferments contained in the alimentary juices, converted into closely allied substances called peptones, the change being in all probability one which depends on the combination of the original proteid substances with the elements of water, so that these bodies probably stand to the peptones in the relation of anhydrides.

From the researches of Plosz ('Ueber Peptone und Ernährung mit denselben,' Pflüger's *Archiv*, IX. 323-329), and of Richard Maly ('Ueber die Zusammensetzung und physiologische Bedeutung der Peptone,' Pflüger's *Archiv*, IX. 585-619), it has been ascertained that the proteid matter required by the animal body may be supplied to it in the form of peptones; from which it results that the organism possesses the power of converting those bodies into the proteid substances which enter into the composition of the tissues.

Little is known of the ultimate end of the albuminous bodies in the organism. It would appear as if the so-called *albuminoid* bodies were their closest derivatives. In their more thorough decomposition in the organism, the nitrogen probably passes into amido-compounds, of which the most completely oxidised, as urea, are excreted. It is, however, very probable from their composition, that fats, glycogen, and sugars take their origin, to a certain extent, in the albuminous bodies, and in support of this view there are weighty physiological facts. Conversely, it appears that synthetic processes of a higher order occur in the organism, whereby albuminous bodies form still more complex compounds (see below, p. 55).

Percentage Composition of the Proteids.—The various bodies belonging to the class of proteids contain their constituent elements in proportions which are limited by the following numbers:—

Carbon	52·7	.	54·5 per cent.
Hydrogen	8·9	.	7·3 "
Nitrogen	15·4	.	16·5 "
Oxygen	20·9	.	23·5 "
Sulphur	0·8	.	1·6 "

All proteids, except peptones, are characteristically colloid, i.e., their solutions possess very slight power of diffusing through animal or vegetable membranes.

The solutions of all proteids deviate the plane of polarised light to the left. The power of deviation exercised by the same weight of the various proteids when in solution in the same volume of water (*specific rotation*) varies for each.

From their solutions the proteids are precipitated under circumstances which vary somewhat in the case of each; sometimes the body which has been precipitated is incapable of re-solution, and must be looked upon as a product of chemical change; at other times it can be re-dissolved. The precipitation of soluble proteids occurs under the influences of heat, acids, and mineral salts, and various organic bodies such as alcohol, tannic acid, &c.

When obtained in a solid form by the precipitation of their solutions, by any of the means above referred to, proteids present at first the appearance of white flocculent matter, heavier than water destitute of crystalline structure.

When solutions of the proteids are dried at a gentle heat, so as to drive off the water in which they are dissolved, or with which they are combined, they appear as translucent and perfectly amorphous solids, which break with a vitreous fracture, and furnish, when triturated, a yellowish-white or white powder.

General Chemical Reactions of the Proteids.—The proteids are all soluble in solutions of the caustic alkalies; the solution then contains compounds of the proteids with the alkali-metals, termed alkaline albuminates; these are decomposed when neutralised by means of an acid, the albuminous substance being then precipitated in a more or less changed condition.

Acetic acid, when concentrated, and with the aid of heat, dissolves all the proteids; the subsequent addition of a solution of potassium ferrocyanide induces a precipitate.

Solutions of proteids are precipitated when treated with acetic acid and an excess of a concentrated solution of a neutral salt such as sodium or magnesium sulphate.

When a solution of the proteids, or the bodies themselves in a solid state, are heated with a solution of mercuric nitrate, containing an excess of nitric acid, in the former case a precipitate first falls, which, on the application of heat, becomes of a purple-red colour; in the latter the solid albuminous body acquires at first an opaque white and then a purple-red colour. This is known as 'Millon's reaction:' it is also exhibited by gelatin and some other allied bodies which do not belong to the proteids proper.

When boiled with strong nitric acid, all the albuminous substances ultimately furnish a yellow solution, which, when treated with an excess of alkalies, becomes of a red amber colour; this is known as the xanthoproteic reaction.

Iodine colours the solid proteids of an intense brownish-yellow colour; the reaction is one which is easily seen by the aid of the microscope.

When subjected to the action of certain of the alimentary juices (gastric and pancreatic juices), the proteids are converted into bodies called peptones, which do not differ perceptibly in chemical composition from the proteids from which they are derived, but which possess marked differences in properties; the peptones, as has been already said, are readily reconverted into proteids in the various tissues and organs of the body.

Decomposition of the Proteids.—1. *Action of Water.*—When heated with water in sealed tubes, at a temperature of 100° C., the proteids are sooner or later dissolved, and then decomposed, peptone-like bodies being at first formed,

and afterwards a number of complex bodies, of which some are soluble in alcohol and ether (A. Gautier).

2. *Action of Heat.*—When subjected to dry distillation, the proteids furnish an oily fluid, long known as Dippel's oil, which contains (1) ammoniacal salts of the fatty acids, as ammonium butyrate, valerate and caproate; (2) amines, derived from the monatomic alcohols, viz. methylamine, propylamine, butylamine, &c.; (3) bodies belonging to the aromatic group, as aniline, and picoline and lutidine; phenol, benzol and its homologues.

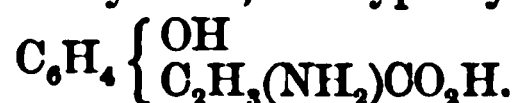
3. *Action of Oxidizing Agents.*—When oxidized by means of manganese dioxide and sulphuric acid or potassium bichromate and sulphuric acid, the proteids furnish bodies belonging to the aromatic and fatty groups. Amongst others the following:—

Acetic aldehyde, hydrocyanic acid, benzoic aldehyde, propionic aldehyde, propyl cyanide, benzoic acid, valerianic aldehyde, butyl cyanide, acetic acid, propionic acid, valerianic acid.

When oxidised by means of chlorine the proteids yield, amongst other products, fumaric acid, oxalic acid, and chlorazol—

Fumaric acid	$C_4H_4O_4$
Oxalic acid	$C_2H_2O_4$
Chlorazol	$C_4H_3Cl_3N_3O_4$

4. *Action of Strong Mineral Acids.*—Prolonged boiling with sulphuric and hydrochloric acids decomposes the proteids, and amongst the products are found glycol, or amido-acetic acid, $C_2H_2(NH_2)O.OH$; leucine, or amido-isocaproic acid, $C_6H_{11}(NH_2)O_2$; and tyrosine, or oxyphenylamidopropionic acid,



The last two of these bodies can be produced by the lengthened action of trypsin upon certain of the albuminous bodies.

When oxidised by nitric acid, the proteids yield first a yellow insoluble body (xanthoproteic acid), which dissolves on further action, paroxybenzoic and oxybenzoic acids ($C_7H_5O_3$) being ultimately formed.

5. *Action of Strong Caustic Alkalies.*—When fused with potassium or sodium hydrate, the proteids yield picoline and pyridine, leucine and tyrosine, and salts of the fatty acids.

Classification of the Proteids.—The proteids which are met with in the animal body, although possessed of certain characters common to the whole, may be divided into distinct groups, according to their solubility in water, their coagulability by heat, their solubility in solutions of sodium-chloride of various strengths, and their precipitation by acids.

I. ALBUMENS.—Proteids which are soluble in water and in very dilute acids, which are not precipitated by addition of common salt in any quantity to their solutions, and which are precipitated from their solutions when these are heated to temperatures between 60° — 70° C. The two varieties of albumens well known are:

a. Serum-albumin. The special characters by which it is distinguished from b. are, (1) its not being coagulated when it is shaken with ether, and (2) its specific rotatory power, which for Fraunhofer's line D = -56° .

b. Egg-albumin, which is precipitated by ether, and which has a specific rotatory power = $-35^\circ.5$.

II. GLOBULINS exist in certain fluids of the body in a state of solution; are precipitated from their diluted solutions by CO_2 ; are coagulated by heat; they are not soluble in pure water, but are soluble in dilute solutions of common salt, from which they are precipitated when salt is added to saturation.

The following bodies belong to the group of globulins:—

(1) *Globulin proper*.—This substance is the chief proteid constituent of the crystalline lens. It possesses all the chemical reactions of (2) and (3), but differs from these in not being coagulated when its solution is mixed with either of them.

(2) *Fibrinogen or metaglobulin* occurs, together with 3, in the plasma of the blood, in chyle, and in serous transudations. Its characteristic reaction is that it is precipitated by the addition of solution of fibrinoplastic substance, *under suitable conditions*, fibrin being formed.

(3) *Fibrinoplastic substance, or Paraglobulin*.—In addition to the chemical reactions of the globulins, this body possesses the characteristic property of being precipitated by the addition of solutions of fibrinogen, fibrin being formed.

(4) *Myosin*. — The juice of flesh contains a body which possesses, when in solution, the reactions of the globulins. The characteristic of this substance is its spontaneous coagulation, when the muscle dies, and becomes acid (see ‘Chemical constituents of Muscle’).

(5) *Vitellin*, the chief albuminous constituent of the yolk of egg. Soluble in 10 per cent. solution of NaCl , from which it is precipitated on addition of water (see p. 55).

III. FIBRIN.—An insoluble proteid, not existing in the living body, but resulting from the union of fibrinogen and fibrino-plastic substances, under suitable circumstances. Is insoluble in water and in dilute acids.

IV. ALBUMINATES.—Substances produced by the action of alkalies upon solutions of the proteids. Not soluble in solutions of common salt. Their solutions are precipitated when neutralised with acids. The precipitation does not take place in the presence of alkaline phosphates.

To this group belong the so-called alkaline albuminates and casein.

V. SYNTONIN, OR ACID-ALBUMIN.—Produced by the action of dilute acid upon the various proteids. Solution is not precipitated by heat. When an acid solution of syntonin is exactly neutralised, the substance is precipitated. Syntonin is insoluble in water and solutions of common salt. It is soluble in weak solutions of the caustic alkalies; from this solution syntonin can be precipitated in an insoluble form by adding magnesium sulphate, and boiling.

VI. PEPTONES.—Under this group are included bodies which are produced when the various proteids are subjected to the action of certain hydrolytic ferments contained in the gastric and pancreatic juices, as well as when they are subjected to other hydrolytic influences.

Peptones are very soluble proteid bodies, which possess to a remarkable degree the power of diffusing through animal membranes. They are not precipitated from their solutions by the mineral acids, nor by the great majority of the mineral salts which precipitate other soluble proteids.

They are precipitated, however, by a large excess of alcohol and by tannic acid.

When solutions of the peptones are treated with small quantities of solution of copper sulphate, and then an excess of solution of sodium hydrate is added, a beautiful pink colour is produced.

In the case of fibrin and fibrin-peptone, Maly has determined that there is no difference in chemical composition to be discovered by elementary analysis (Maly, 'Ueber die chemische Zusammensetzung und physiologische Bedeutung der Peptone,' Pflüger's *Archiv*, IX. 585-619).

Though apparently identical in most of their characters, the products of the action of ferments upon the proteids appear to be various. Thus the complex proteid molecule appears, according to the researches of Kühne, to give rise, under the influence of the gastric and pancreatic ferments, to bodies which, though on superficial examination appearing identical, are in reality distinct. These bodies belong to two classes; those belonging to the first, or *anti-peptone* class, are not capable of undergoing further change under hydrolytic influences; those belonging to the second, or *hemi-peptone* class, ultimately give rise, under favourable circumstances, to leucine and tyrosine (*Verhandlungen des naturhist. med. Vereins zu Heidelberg*, 1876). For further information relating to this subject the reader is referred to Chapter III.

B. The Albuminoid Bodies.

These substances, which occur as important constituents of many tissues, and approach the albuminous bodies in composition (although some of them contain no sulphur), are looked upon as their nearest derivatives, though we do not know by what processes they arise from them.

They differ from one another much more than the albuminous bodies, and, if we except their colloidal character, i.e. their inability to crystallize and to form true solutions, they possess no common character. Under hydrolytic influences they furnish the same products as the albuminous bodies, viz. leucine and tyrosine, in large quantities. One of these bodies, chondrin, which is said

to yield grape sugar when it is boiled with dilute sulphuric acid, is probably a glucoside, and should therefore be separated from the other substances.

The most important albuminoid bodies are—

a. Mucin (C 52·2, H 7·0, N 12·6, O 28·2 per cent.) forms a viscid fluid with water (mucus), which is precipitated by a little acetic acid, and by excess of alcohol. It occurs in mucous secretions, and in gelatinous connective tissue (Wharton's jelly, &c.) Besides leucine, it yields much tyrosine.

b. Glutin, gelatin (C 50·4, H 6·8, N 18·3, S + O 24·5) is extracted from nearly all the connective tissues (bones, ligaments, skin) by boiling them with water. Gelatin swells in cold water; by boiling, a solution is obtained which again gelatinizes on cooling. On prolonged boiling it splits up into a non-gelatinizing peptone, which also is a product of digestion. Hydrolytic treatment furnishes leucine, glycosine, and ammonia, but no tyrosine.

c. Sericin, or silk-gelatine ($C_{15}H_{25}N_5O_8$?) is a constituent of silk.

d. Keratin (C 50·3—52·5, H 6·4—7·0, N 16·2—17·7, S 0·7—5·0, O 20·7—25·0 per cent.) is the residue left when the so-called horny tissues have been treated with ether, alcohol, water and acids: it is a substance only soluble in hot alkalies, and which swells up in cold alkalies. It yields 10 per cent. of leucine, and 3·6 per cent. of tyrosine.

e. Elastin (C 55·5, H 7·4, N 16·7, O 20·5 per cent.) is the residue left after the removal of all soluble matters from connective tissue; it is the *characteristic substance of all elastic tissues*. It is insoluble in all agents which do not decompose it.

It yields much leucine (36—45 per cent.), but little tyrosine ($\frac{1}{8}$ per cent.)

f. Fibroin (C 48·6, H 6·5, N 17·3, O 27·6 per cent.) is the chief constituent of silk, and is soluble in concentrated acids and alkalies.

C. Bodies more Complex than the Proteids.

We can only certainly assume the existence of bodies of this class from the fact that when decomposed they yield, amongst other products, proteids. To this group belong:

1. *Hæmoglobin*, the red crystalline colouring matter of the blood corpuscles, which is likewise contained in small quantities in serum and in the muscles. Its properties will be described in the chapter on Blood (pp. 61 and 70).

When hæmoglobin is decomposed by acids or alkalies, it splits up into a red iron-containing body called hæmatin, and a proteid substance.

2. *Vitellin* is an albuminous substance which is separated from

yolk of egg by a 10 per cent. solution of sodium chloride, and which is precipitated from the salt solution on the addition of water.

As, when coagulated, vitellin yields a proteid substance and lecithin, it is looked upon as probably being a complex body of which these are products of decomposition. There are no grounds for arriving at a certain opinion on this matter.

3. *Ichthin* (obtained from the ova of the sturgeon), *Ichthidin* (obtained from carp's eggs), and *Emidine* (obtained from the eggs of the tortoise), appear to be similarly constituted to Vitellin.

4. *Nuclein*.—Probably connected more or less remotely with the above bodies, is the substance described by Miescher and Hoppe-Seyler as a constituent of the nuclei of pus corpuscles, and called by him nuclein (Miescher, 'Ueber die chemische Zusammensetzung der Eiterzellen,' *Med.-chem. Untersuchungen von Hoppe-Seyler*, Heft 4, 1871, § 441; Hoppe-Seyler, 'Ueber die chem. Zusammensetzung des Eiters,' *Ibid.*, § 486 *et seq.*)

Nuclein is separated from pus corpuscles by extracting them with hot alcohol and afterwards digesting the undissolved substances in artificial gastric juice, which dissolves the proteids and leaves the proper substance of the nuclei—nuclein—undissolved.

It is soluble in weak solutions of sodium hydrate, from which it is precipitated by hydrochloric acid.

Nuclein possesses some properties which resemble those of mucin; it differs from the latter substance in containing 9.59 per cent. of phosphorus.

This very imperfectly-known body is said to be a constituent of yeast (Hoppe-Seyler, *op. cit.*) and probably of the nuclei of the blood corpuscles of birds and amphibia (see Plósz, 'Ueber das chemische Verhalten der Kerne der Vogel- und Schlangenblutkörperchen,' Hoppe-Seyler's *Med.-chem. Untersuchungen*, Heft 4, § 461).

With the exception of the above, no other bodies having a more complex constitution than the albuminous have yet been demonstrated to exist. Nevertheless, it appears in the highest degree probable that such a body exists in the muscle, one of whose products of decomposition is myosin.

D. Glucosides which contain Nitrogen.

The following nitrogenous glucosides have been discovered in the human organism :—

1. *Protagon* (C 67.21, H 11.59, N 2.70, P 1.5, O 17.0 per cent.) This body is probably the chief proximate phosphorized constituent of brain (Liebreich, *Annalen der Chemie und Pharmacie*, Bd. 94, 1865–6, pp. 29–34), and can be obtained in a perfectly crystallized condition. It contains 1.5 per cent. of phosphorus. Under the influence of hydrolytic agencies it yields the products of decomposition of lecithin (neurine, glycerin-phosphoric acid, and stearic acid), but in addition considerable quantities of a lævo-rotatory sugar. According to Diakonow (*Centralblatt f. d. med. Wissenschaft*, 1868, § 97) and Hoppe-Seyler (*Med.-chem. Untersuchungen*, Heft 4, § 487, 'Ueber die phosphorhaltigen

Substanzen des Eiters'), protagon is a mixture of lecithin with a glucoside, *Cerebrin* $C_{17}H_{33}NO_3$ (?)

Protagon is insoluble in water, but swells into a viscid mass; it is soluble in hot alcohol, from which it is deposited—if allowed to cool very gradually—in the form of clusters of needle-shaped crystals.

2. *Chondrin* (C 49·9, H 6·6, N 14·5, S 0·4, O 28·6 per cent.) is extracted from hyaline cartilage and the covering of the holothuria by boiling with water; in its external characters it resembles gelatin. Under hydrolytic treatment it furnishes leucine and grape sugar (the latter fact is disputed).

3. *Chitin*, a nitrogenous glucoside, is contained in the shell or exoskeleton of arthropoda.

4. *Hyalin* is a nitrogenous glucoside found in the cysts of echinococci.

5. *Indican*. This body has already been referred to (p. 48).

E. The Ferments of the Organism.

Ferments are bodies which, by an action which is yet unknown, cause a decomposition of bodies in proximity to them without being themselves consumed. Certain ferments cause the bodies which are decomposed to combine with the elements of water, and their action may therefore be designated as *hydrolytic*. The ferments of the animal body are often designated *unorganized*, to distinguish them from certain elementary organisms which, possessing the power of setting up certain decompositions (fermentations) in bodies with which they are brought in contact, are termed *organized* ferments.

Unorganized ferments are distinguished from organized (*a*) by the fact that they may be dissolved in certain menstrua, and that their solutions admit of being filtered without any impairment of ferment action; (*b*) by the fact that their action is not prevented or inhibited by many agents, such as salicylic acid (Kühne), which at once arrest the action of organized ferments.

Some, at least, of the ferments of the body seem to be derived from, or to originate in, other bodies, which may be termed 'zymogens.' The latter, being formed in secreting organs, appear under favourable circumstances to furnish active ferments (Heidenhain, Kühne).

The animal body contains the following groups of hydrolytic ferments:—

a. AMYLOLYTIC, OR SUGAR-FORMING FERMENTS, which convert starch, glycogen, &c. into sugar, with absorption of water; these ferments are present in saliva, pancreatic juice, in the liver, and many other organs.

β. FAT-DECOMPOSING FERMENTS, which cause fats to combine with the elements of water and to decompose into fatty acids and glycerin; a ferment of this class appears to exist in the pancreatic juice.

γ. PROTEOLYTIC FERMENTS. These ferments, which exist in the gastric juice (pepsin) and in pancreatic and intestinal juices, convert soluble and coagulated albuminous bodies into peptones; one of these ferments (trypsin) effects a further decomposition into leucine, tyrosine, &c.

No other but hydrolytic ferments have yet been discovered in the body.

In the foregoing pages the chemical constituents of the animal body have been classified according to their chemical affinities. Other methods of classification are based on the origin of these substances in the body, but they are necessarily unsatisfactory, in consequence of the slight acquaintance which we possess with the chemical processes of the organism.

The basis of the most commonly adopted arrangement is the fact that from the albuminous bodies, the carbohydrates and the fats, which form the chief organic food of the body, all its constituents are derived. The changes which each substance undergoes in its conversion into a formed element of the body are included in the term *assimilation*, or 'progressive metamorphosis;' whilst the further changes which end in excretion are included in the term 'retrograde metamorphosis.' Processes of oxidation and decomposition play the principal part in bringing about the latter; complicated breaking up into more and more simple bodies, the chief representatives of which are carbonic acid, water, urea, sulphuric and phosphoric acid.

The chemical processes which are concerned in the so-called 'progressive metamorphosis,' and which lead to the formation of albuminoid bodies, of hæmoglobin, of protagon, &c., are altogether unknown to us, although we may doubtless conclude that in their production synthetic processes play some part.

CHAPTER I.

THE BLOOD AND ITS CIRCULATION.

THE material interchanges which take place between the constituents of the body and the external world, and between these constituents themselves, occur through the medium of a fluid which is in perpetual contact with the remotest parts of the body, as well as with those apparatuses which are to be considered as the portals by which the body communicates with the exterior; that fluid is the blood.

The blood receives directly from the external world oxygen and nutritive matters, and from it the individual *tissues* obtain these substances. The latter, again, rarely give up their excrementitious products *directly* to the external world, but pour them, first of all, into the blood, which throws them out of the body at certain destined places. The blood, moreover, is continually taking up substances which have undergone changes in different localities, and deposits them, for further use, elsewhere.

Every particle of the body which plays a part in its chemical changes must therefore, repeatedly, presumably very frequently, become the constituent of a very voluminous fluid (the blood), in which it mixes with innumerable other substances.

It is expedient, in the exposition of the chemical changes which occur in the body, to consider the blood as its natural centre, and to classify the various processes as sources of expenditure or gain to the blood, before treating of the interchanges between the matter of the whole organism and the external world.

I. THE BLOOD.

Human blood is a red fluid, opaque even when in very thin layers, and possessed of an alkaline reaction. Its specific gravity is, in health, about 1055. It consists of a yellow alkaline liquid (liquor, or plasma, sanguinis), and small microscopic bodies, the blood corpuscles, which are suspended in the fluid in large numbers (4 to 5·5 millions in one cubic millimetre; Welcker¹), and are in close contact with one another. These are mostly red,

¹ Welcker, *Prag. Vierteljahrsschr.* Bd. iv. p. 11.

but a small number (1 in 500 or 1 in 300, Welcker¹—in the splenic veins, however, 1 in 70, Hirt²) of colourless corpuscles are mixed with them.

To test the alkaline reaction of blood the mere employment of litmus paper is not sufficient: either the colourless diffusate obtained by means of a porous septum and distilled water is tested (Kühne), or a drop of blood is placed on litmus paper which has been previously moistened with a solution of common salt (Zuntz).³

The determination of the number of the blood corpuscles is best done by the method of Malassez.⁴ Blood is diluted with 100 times its volume of an indifferent fluid [10 per cent. solution of sodium sulphate], and introduced into a very fine glass tube, the sides of which have been flattened so that its section is elliptical; the cubic contents of a unit-length of this tube being known, the blood corpuscles contained in it are counted under the microscope with the aid of a peculiarly ruled eye-piece micrometer.

Red Blood Corpuscles.

In man, the red blood corpuscles have the form of circular biconcave discs; their greatest diameter averages $\frac{1}{128}$ mm. They are uniformly coloured red. They are very soft, ductile, and elastic; neither membrane nor nucleus can be detected, so that they cannot be designated cells.

The blood corpuscles of mammalia, with the exception of the elliptical ones of the camel, are similar to those of man; in birds they are elliptical and biconvex; in amphibia elliptical, flat, and very large (in *Proteus* the diameter is actually $\frac{1}{16}$ mm); in fishes they are mostly of a rounded elliptical form. In birds, amphibia, and fishes, they have *nuclei*. In the invertebrata red blood corpuscles are only present in a few classes. Almost all invertebrata, and, amongst vertebrata, *Amphioxus lanceolatus*, have colourless or yellowish blood, with colourless corpuscles of various shapes; a few, however, have red blood with colouring matter similar to that of vertebrata.

The specific gravity of blood corpuscles is somewhat greater than that of the plasma; for if not prevented (by coagulation, &c.) they sink to the bottom of blood which is undisturbed. When blood is at rest, the red corpuscles have a tendency to aggregate into piles, like *rouleaux* of coins. The cause of this phenomenon is unknown.

The presence of red corpuscles is the cause not only of the red colour, but also of the opacity of the blood. By a variety of means the red colouring matter can be extracted from the blood corpuscles, when it dissolves in the plasma and colours it red; the blood becomes in consequence transparent when examined in thin layers ('lake-coloured,' Rollett), but at the same time, darker, owing to the absence of reflection from the concave red discs. Conversely, the blood becomes of a brighter red when the blood

¹ Welcker, *Wien. med. Wochenschrift*, 1854, Nr. 8.

² Hirt, *Archiv f. Anat. u. Phys.* 1856, p. 174.

³ Zuntz, *Centralblatt f. d. med. Wissenschaften*, 1867, Nr. 34.

⁴ Malassez, 'De la numération des globules rouges du sang,' *Comptes Rendus*, 2 déc. 1872.

corpuscles are shrivelled up by the addition of salt, so that the reflected light becomes more concentrated. The corpuscles in the process of decolourization swell up from their margins (Hermann) and finally become globular; the decolourized and very pale residue of the corpuscles is called the *stroma* (Rollett¹).

The means of decolourizing the blood corpuscles, previously referred to, are dilution of the blood with water: alternate freezing and thawing of the blood (Rollett): the transmission of electric shocks (Rollett): removal of the gases of the blood: treatment with salts of the bile acids (v. Dusch), ether (v. Wittich) chloroform (Böttcher), small quantities of alcohol (Rollett), or carbon disulphide (Hermann). All these processes, except the first named and the removal of the gases of the blood, not only effect the decolourization of the corpuscles, but subsequently lead to the solution of the stroma in the plasma, a glutinous nucleus being sometimes left.

By the action of boracic acid on the nucleated corpuscles of amphibia, a red mass containing the nucleus is separated from the residual colourless stroma; we must therefore admit that the former contractile mass ('the Zooid') is infiltrated in the pores of the colourless stroma (the 'Oceoid,' Brücke).

A similar deportment is observed in the case of the non-nucleated blood corpuscles of mammalia (Roberts,² Stricker). Some consider these changes, which are produced in numerous other ways, as due to coagulation (Rollett).

The chemical constituents of the red blood corpuscles are :

1. A red colouring matter containing iron, called Hæmoglobin (syn. hæmatoglobulin, hæmatocrystallin), having approximately the following percentage composition: C 54·0, H 7·25, N 16·25, Fe 0·42, S 0·63, O 21·45.

It is slightly soluble in water, but much more readily soluble in weak alkaline solutions. It is not known whether hæmoglobin impregnates the colourless residue of the zooid of the blood corpuscles, or whether it exists in a state of chemical combination with it.

Hæmoglobin is a coloured albuminous compound, and is therefore a body of most complex structure. It readily splits up into an albuminous body, apparently closely connected to globulin (although, unlike the latter, it is not dissolved by oxygen), and a colouring matter, hæmatin. This decomposition is effected by all agents capable of coagulating or precipitating albumin (heat, alcohol, mineral acids), and, besides, by the weakest acids (even by carbonic acid in the presence of much water, and by strong alkalies. Different red-blooded animals possess different kinds of hæmoglobin, which have hitherto only been found to differ in their crystalline form.

Crystals of hæmoglobin, the so-called *blood-crystals*, occur principally in the form of rhombic prisms or tablets; rarely, as in the blood of the guinea-pig, in

¹ Rollett, 'Vers. und Beobacht. u. d. Blut,' *Wien. Sitzungsber. M. natw. Cl. Abth. II.*, Bd. xlv. p. 65.

² Roberts, 'On the Effects of Magenta and Tannin on the Blood Corpuscles,' *Proc. Royal Soc.* 1863, p. 481.

the form of rhombic tetrahedra. Those crystals may be obtained by destroying the blood corpuscles (by means of water, ether, salts of the bile acids), and evaporating or cooling the lake-coloured fluid which results. Crystals are easily obtained from the blood of dogs, horses, guinea-pigs, and birds; with difficulty or not at all from that of oxen and pigs.

The coloured product of the decomposition of hæmoglobin, Hæmatin ($C_{68}H_{70}N_8Fe_2O_{10}$ (?) Hoppe-Seyler ¹), which does not occur uncombined in the body, is a crystalline colouring matter, which, when dried, has a bluish-black colour and a metallic lustre; it is insoluble in water and alcohol, but soluble without decomposition in aqueous or alcoholic solutions of acids and alkalies. Its acid solutions are brown; its alkaline solutions are dichroic, appearing green in thin and red in thicker layers.

Solutions of hæmatin, when examined with the spectroscope, exhibit an absorption band in the red, the position of which is different in acid and alkaline solutions. When treated with reducing agents, two new absorption bands, situated close to each other in the yellow, make their appearance; these are not to be confounded with the two bands of O-hæmoglobin (see p. 69). Hæmatin crystallizes from solutions in glacial acetic acid in the form of rhombic plates, which in the presence of chlorides are composed of hydrochlorate of hæmatin (Hoppe-Seyler ²); these so-called hæmin-crystals may serve for the detection of blood (Teichmann ³).

By the action of concentrated mineral acids iron is separated from hæmatin; the resulting colouring matter bears the name of 'iron-free hæmatin' (Mulder and van Goudoever ⁴), hæmatoporphyrin ($C_{68}H_{74}N_8O_{12}$ (?) Hoppe-Seyler ⁵), hæmatoin (Preyer).

According to recent accounts (Hoppe-Seyler ⁶), when hæmoglobin is decomposed in the absence of air, a purple body, with four absorption bands, 'hæmo-chromogen,' is formed; the action of oxygen immediately converts it into hæmatin.

In the organism hæmoglobin gives rise to coloured products other than the artificial ones, as hæmatoidin, bilirubin, &c. (For these consult Chapter II., under the heads of Bile, Urine, &c.) For the deportment of hæmoglobin towards gases, and for its optical properties, see below.

2. An albuminous body, precipitable by carbonic acid, but soluble on the passage of air through the fluid, *globulin*.

The nuclei of the blood corpuscles consist of a substance resembling mucin (Brunton ⁷).

The observations of Plósz ⁸ seem to show that the chief constituent of the nucleus is an organic body containing phosphorus, and probably identical with the *nuclein* of Miescher.

3. Small quantities of substances soluble in ether: fats, soaps,

¹ Hoppe-Seyler, *Beiträge zur Kenntniss des Blutes u. s. w.: das Hæmatin*, 'Med.-chem. Untersuchung.', Heft ii. p. 525.

² Hoppe-Seyler, *loc. cit.*

³ Teichmann, *Zeitschrift f. rat. Med. N. F.* Bd. iii. p. 375; Bd. viii. p. 141.

⁴ Mulder und Van Goudoever, *Journ. f. prakt. Chem.* 1844, Bd. xxxii. p. 186.

⁵ Hoppe-Seyler, *loc. cit.* p. 533.

⁶ Hoppe-Seyler, *Med.-chem. Untersuchungen*, Heft iv. p. 540.

⁷ Brunton, *Journal of Anatomy and Physiology*, Nov. 1869.

⁸ Plósz, *Med.-chem. Unters. von Hoppe-Seyler*, Heft. iv. p. 461.

cholesterin, protagon, and its products of decomposition (lecithin, glycerin-phosphoric acid, &c.)

4. Salts, especially compounds of potassium, and of phosphoric acid.

5. Water.

6. Gases.

Colourless Blood Corpuscles.

The colourless blood corpuscles (lymph corpuscles) are globular, nucleated cells, with a somewhat granular, mulberry-shaped surface; they are larger than the red corpuscles, having a diameter of about $\frac{1}{100}$ mm. They show the greatest resemblance to the cells of the lymph, from which they are derived. At the temperature of the body these cells, which are destitute of a cell wall, exhibit lively movements, throwing out processes and drawing them in again, whereby they can drag into their interior foreign particles; these cells also possess the power of subdividing (Klein). Their chemical composition has not yet been exactly determined; it is probably very similar to that of the red corpuscles without the pigment. There are grounds for believing (Chapter V.) that the colourless blood corpuscles are precursors of the red, as transition forms between white and red corpuscles are found in certain situations (for example, in the blood of the splenic veins).

Blood Plasma or Liquor Sanguinis.

For the separation of the plasma of the blood see below (under 'Death of the Blood'). The reaction of blood plasma is, like that of blood itself, alkaline. The chemical constituents of the plasma are:

1. Water, about 90 per cent.

2. Proteids, viz.:

a. Albumin (precipitated by heat).

β. Sodium albuminate ('serumcasein,' precipitated by acids).

γ. The substances which form fibrin during coagulation of the blood.

The greater portion of the albuminoid substances consists of albumin; altogether they form from 8-10 per cent. of the plasma.

3. Creatine, hypoxanthine, and urea: also at times hippuric and uric acids, in very small quantities.

4. Grape sugar in small quantities, varying according to the situation (see Chapter V.)

5. Fats, soaps, fatty acids, cholesterin, lecithin. The fat is partly dissolved by the soaps, and partly exists as an emulsion, but always in a small, though varying, quantity (0.1—0.2 per cent.)

6. An odoriferous principle peculiar to each kind of blood.

7. A *yellow pigment*. (The serum also often contains hæmoglobin, but this may be only an impurity, caused by disintegrated blood corpuscles.)

8. Salts, in which salts of sodium, chlorides, and carbonates preponderate; therefore more especially common salt and carbonate of sodium.

9. Gases.

With the exception of the bodies included under 2, the above-named constituents form also the constituents of the serum—that is, of the liquid obtained after the coagulation of the blood or plasma.

The Gases of the Blood.

The gases contained in blood are oxygen, carbonic acid, and nitrogen, which are partly absorbed, and partly in loose chemical combinations (Magnus,¹ Lothar Meyer,² Ludwig³).

The following table exhibits the total amount and the relative proportion of these gases contained in 100 volumes of arterial blood of the dog (Pflüger⁴).

	At 0° C. and 0 ^m 76 pressure.	At 0° C. and 1 met. pressure.
Total gases	59·0 vols.	44·9 vols.
Oxygen	22·2 „	16·0 „
Carbonic acid	35·0 „	26·6 „
Nitrogen	1·8 „	1·4 „

The fundamental law of the absorption of gases by liquids (Henry's, Dalton's, and Bunsen's law) may be expressed as follows:—The unit of volume of a liquid at a given temperature absorbs a definite volume of a gas; the latter is designated the *coefficient of absorption of the liquid for the gas*. The coefficient of absorption decreases as the temperature increases, according to a law which varies for each liquid and gas; at the boiling point of the liquid the coefficient of absorption is equal to 0.

The *volume* of gas taken up, therefore the absorption coefficient, is independent of the pressure, whilst the *weight* of the gas taken up by a fluid is directly proportional to it.

As different gases existing in a gaseous mixture exert no pressure upon one another, we must in the preceding sentence understand pressure to signify the

¹ Magnus, 'Ueber die im Blute enthaltenen Gase, Sauerstoff, Stickstoff und Kohlensäure,' *Poggendorff's Annalen*. 1837, p. 588.

² Lothar Meyer, 'Die Gase des Blutes,' *Zeitschrift f. rat. Med. N. F.* Bd. viii. p. 257. 1857.

³ Ludwig's contributions to our knowledge of the gases of the blood have been mainly published through the medium of his pupils. The following are the references to at least the chief of the memoirs published by them: Setschenow, *Sitzungsber. d. Wien. Ak. M. natw. Cl.* Bd. xxxvi. p. 293; *Zeitschr. f. rat. Med. R.* III. Bd. x. p. 101, Bd. xxiii. p. 16; Schoeffer, *Sitzungsber. d. Wien. Ak.* Bd. xli. p. 519; *Centralbl. f. d. med. Wissensch.* 1866, p. 657; Sachs, *Arch. f. Anat. u. Phys.* 1868, p. 845; Sczelkow, *ebendas.* 1864, p. 516; *Sitzungsber. d. Wien. Ak.* Bd. xlv. p. 172; Preyer, *ebendas.* Bd. xlix. p. 27; *Centrbl. f. d. med. Wissensch.* 1866, p. 321, 1867, p. 278; Holmgren, *Sitzungsber. d. Wien. Ak.* Bd. xlviii. p. 614; A. Schmidt, *Ber. d. k. sächs. Ges. d. Wissensch. M. ph. Cl.* 1867, p. 80, u. 99.

⁴ Pflüger, 'Die normalen Gasmengen des arteriellen Blutes nach verbesserten Methoden,' *Centralblatt für die med. Wissenschaften*, October 26, 1868.

partial pressure of the particular gas. Thus water absorbs only as much oxygen from the atmosphere as corresponds to the partial pressure of the oxygen contained in it, viz. about $\frac{760}{5} = 152^{\text{mm}}$ Hg.

Absorbed gases can therefore be expelled from a liquid, 1. By placing it in a vacuum which is being continually renewed. 2. By placing it in a space which is free from the gas to be expelled, and which is maintained free. 3. By raising the temperature of the liquid to boiling point.

Certain gases form chemical compounds with certain bodies (in the relations of their equivalents), which, however, undergo DISSOCIATION when they are placed in a space where the partial pressure of the gas falls below a certain limit. This minimum pressure, which is an essential condition to the persistence of the combination, is, for each special case, a *constant*, which, still, like the coefficient of absorption, decreases as the temperature increases. From these loose chemical combinations the gas can, therefore, be driven as from simple solutions (viz. by the vacuum, by foreign gases, or by the action of heat). These loose compounds of gases are distinguished, however, from simple solutions, in that by increasing the partial pressure of the gas beyond a certain limit, the quantity taken up by the liquid no longer increases.

There are some bodies which form loose chemical compounds with gases dissolved in a liquid, so that the solution may contain a chemical compound of the gas as well as a portion simply dissolved. In such a case the weight of the gas dissolved is partly proportional to the pressure, and partly independent of it.

The quantity of gas by weight taken up by a solution is dependent on the partial pressure of that gas outside the fluid, because each gas which is dissolved by a liquid possesses, at the surface of the latter, a tension, in virtue of which it tends to escape. If this tension is equal to the partial pressure of the gas in the space above the liquid, equilibrium is established; if it is greater or less, a passage of gas outwards or inwards occurs, until a condition of equilibrium is attained. In the condition of equilibrium, which is always established sooner or later (and which is hastened by shaking together the liquid and gas), the partial pressure of each gas in the space surrounding the liquid expresses directly the tension of the same gas in the fluid. If we carry the idea of tension into the statement of the laws which have been previously announced, these may be expressed as follows. 1. In the case of purely physical absorption, the tension of a dissolved gas is (*a*) dependent upon the nature of the fluid and the gas, (*b*) proportional to the amount, by weight, which has been taken up, (*c*) dependent upon the temperature—with which it in general increases. 2. If a fluid contain a body which forms a loose chemical compound with a gas, the tension is not proportional to the total quantity of gas taken up, but only to the excess above the quantity which is required to saturate the combining body; if the body, on the other hand, is not saturated, fresh absorption of the gas leads to no increase of tension, but the latter remains equal to the above-mentioned minimum pressure, which, however, varies with the temperature.

[Separation and Determination of the Gases of the Blood.]

In order to separate, whether for qualitative or quantitative analysis, the gases contained in the blood, a known volume of the fluid is boiled in the vacuum obtained by means of a mercurial pump. In consequence, however, of the consumption of oxygen which goes on in the blood after its withdrawal from the body, it is necessary, if it be desired to ascertain the real amount of its gases, that these should be separated either immediately after it has left the body, or that the blood should be preserved in ice until the time when the gases are separated.

The processes employed by various physiologists in these researches differ

considerably; preference is, however (in the opinion of the editor), to be given to the procedure employed by Pflüger and his school.

The annexed diagram represents a mercurial pump according to Pflüger's model, constructed by Geissler, of Berlin, and provided with the apparatus requisite for the separation of the gases of the blood.

FIG. 1.

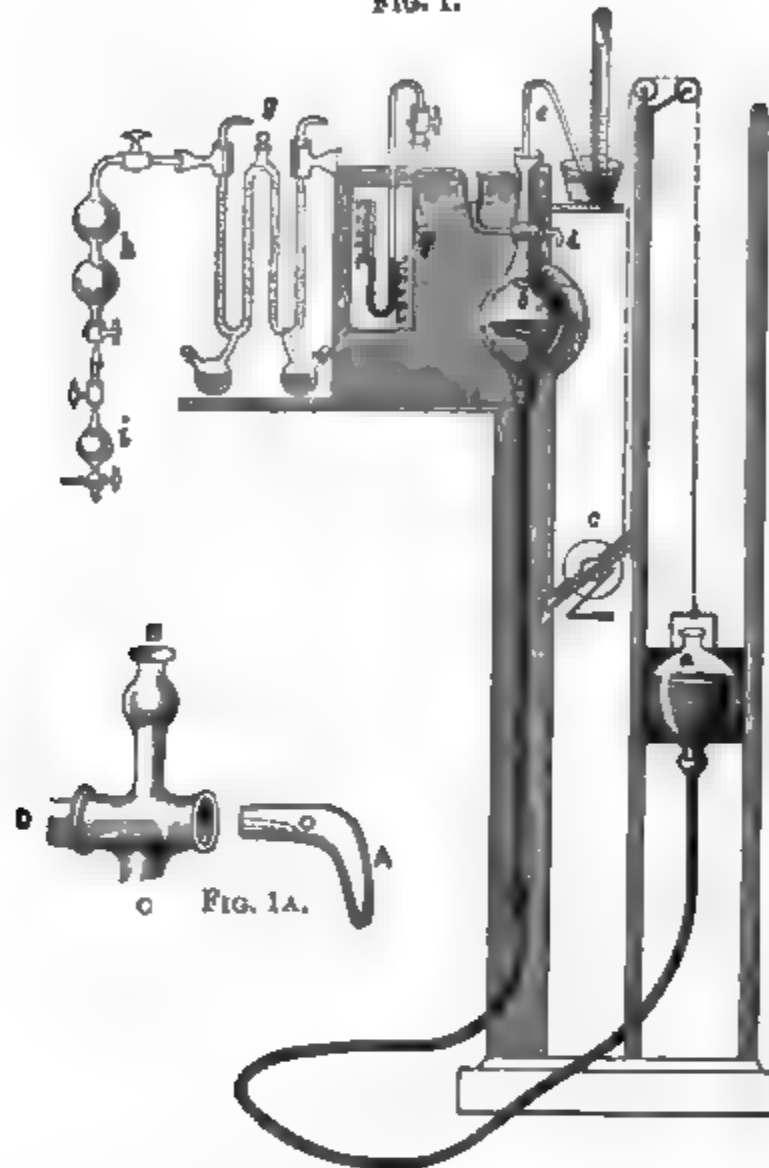


FIG. 1. GEISSLER'S MERCURIAL PUMP FOR THE EXTRACTION OF THE GASES OF THE BLOOD.—*a*, filling-globe connected by means of elastic tubing with the glass tube upon which is blown *b*, the barometer-bulb, which has at its upper part the three-way stopcock *d*; *e* is a glass tube, which is perfectly ground into a tube leading from stopcock *d*; *f* is a mercurial gauge; *g* is the drying apparatus, containing sulphuric acid; *h* is the froth chamber, with two large bulbs blown upon it; *i* is the bulb in which the blood is boiled.

FIG. 1A. ENLARGED DRAWING OF THE THREE-WAY STOPCOCK MARKED *d* IN FIG. 1.—*A* is the plug of the stopcock; *c* is the upper contracted part of the barometric chamber; *B* is the tube into which the gas-delivery tube (*e* in fig. 1A) fits.

c, *d*, *b*, *a*, represent parts of the pump proper; *b* is the barometric chamber of about two litres capacity, provided at *d* with a three-way cock, which enables the chamber to be shut off or placed in communication either with the chambers to be exhausted, *g*, *h*, *i*, or with the open air, or by means of the glass gas delivery tube *c* with a mercurial pneumatic trough. *a* is a bulb larger than

b, and communicating with it by means of a stout caoutchouc tube covered externally with a stout woven fabric, so as to enable it to resist considerable internal pressure without dilating. *a* is contained in a box which may easily be wound up and down by means of the ratchet-wheel *c*, and the band and pulley connected with it.

Mercury is poured into the filling-globe *a*, when the latter is in its lowest position. By winding *a* up until its level is above that of *b*, and placing the stopcock *a* in such a position that *b* communicates with the external air, the bulb *b* is nearly filled with mercury. The stopcock *d* is then turned so as to shut off *b* completely from communication above. On now bringing *a* down to its initial position, viz., about a metre below *b*, the mercury in the latter sinks until it stands at the height of the barometer above the mercury in the reservoir *a*. There is then a Toricellian vacuum in *b*. By a suitable turn of the three-way cock *d*, the chamber *b* is now brought into communication with the apparatus to be exhausted. After the gas contained in the latter has diffused into the chamber, the stopcock *d* is shut, the globe *a* is elevated, and by a suitable movement of the stopcock the imprisoned gas is allowed to pass either into the air, or is collected through *e* over mercury in the pneumatic trough. By repeating several times the series of operations described the amount of residual gas in the apparatus sinks to an insignificant amount, and without great labour a practically perfect vacuum is obtained.

The accessory apparatus shown in the drawing requires description. *f* is a mercurial gauge, *g* is the drying chamber, composed of four glass tubes communicating below with two small reservoirs. The tubes are filled with pumice-stone, or asbestos saturated with sulphuric acid, and the bulbs also contain some of the same acid. The drying-chamber is in communication with two large glass bulbs *h*, which are intended to arrest the froth which arises from the boiling blood. To the 'froth-chamber' is carefully attached a glass bulb *i*, into which the blood is placed. This bulb has at its upper part a single-way stopcock, but below it is provided with a two-way cock. The plug of the stopcock is in the drawing shown to be prolonged considerably beyond the socket into which it fits. This plug is perforated in its long diameter by a canal which passes through it obliquely, and is so arranged that the fluid passing through the canal may be directed upwards into the 'blood-bulb,' or downwards.

A vacuum having been made in the 'drying-chamber,' the 'froth-chamber,' and the 'blood-bulb,' the plug of the lowest stopcock of the blood-bulb has attached to it a piece of thoroughly sound black elastic tube, which is connected peripherally with a glass cannula which is tied into the blood-vessel whence the blood is to be drawn, or preferably with one branch of a three-way stopcock of a blood-measuring tube, which is interposed between the blood-vessel of the living animal and the blood-bulb.

Blood is now allowed to flow through the elastic tube until the latter is filled, the plug being placed in such a position that the displaced air and the displacing blood flow at first not into the blood-bulb but outwards. At a given moment the stopcock is turned so as to open a communication between the blood-bulb and the blood-measuring tube, or the blood-vessel; the blood flows into the vacuous bulb, and immediately enters into ebullition. As soon as enough blood has entered, the lower stopcock is shut, and the stopcocks which shut off the upper part of the blood-bulb from the drying-chamber and the barometric chamber of the pump, are opened. The blood-bulb *i* is now immersed in a vessel containing water at 40° C, when the blood enters into violent ebullition: if arterial in colour before being introduced into the bulb, it assumes almost instantly the cherry-red colour which is characteristic of reduced hæmoglobin; if the reddened walls of the froth-chamber be viewed through a spectroscope the simple broad band of reduced hæmoglobin is then seen. After a few minutes the gases which have been given off are collected over mercury in a tube filled with mercury, the vacuum is renewed, and the process of ebullition continued.

The special features of the process described above, and which renders it preferable to others employed for the same purpose, are (1) the blood may readily be brought directly, without previous defibrination, from the blood-vessels into the apparatus where its gases are separated; (2) the blood is at once introduced into a very large vacuous space, so that the O-pressure outside the blood is always very much below the dissociation tension of the O of the blood, and the latter therefore escapes very rapidly; (3) the vacuum is kept in a dry condition by the sulphuric acid in the drying-chamber; this appears to have very great influence in facilitating the escape of gases from the blood.

Having separated and collected the total gases given off by a known volume or weight of blood, these are measured and analyzed.]

In order to determine whether gases are in a state of simple solution or of loose chemical combination in the blood, either absorption experiments must be made under different pressures, with blood which has been freed from gases, or determination of tension must be made. The methods for effecting the latter, which are of special importance in reference to the chemistry of respiration, will be given in Chapter IV.

1. *Oxygen* gas is found in arterial blood, on an average, in the proportion of 16·9 volumes per cent. (the gas being calculated under a pressure of 1 metre and 0° C) (Pflüger)¹: the amount of oxygen in venous blood varies greatly (Chapter IV.); in venous blood from muscles in a state of rest the amount was found to be only 5·96 volumes per cent., taking an average of five determinations. The deportment of blood, which has had its gases removed, towards oxygen, shows that the latter is not merely absorbed by the blood, *but for the most part chemically combined with it*. The amount (by weight) of the oxygen taken up by blood is almost entirely independent of pressure, and does not therefore follow Dalton's law. But if the blood corpuscles are removed, and simple blood plasma be taken, or (since the latter is difficult to obtain, and immediately coagulates, whilst as regards combination with O the fibrin-formers may be considered as unimportant), instead of plasma, plain serum (page 64), be agitated with oxygen, the gas is merely absorbed (L. Meyer). It follows from this that the oxygen of the blood is chemically combined with a substance contained in the blood corpuscles, but is only absorbed by the plasma or serum (that is, by the water they contain, for serum absorbs just so much oxygen as pure distilled water²). This proposition must likewise be applied to the oxygen normally present in the blood.

Hæmoglobin is the substance which forms the loose chemical

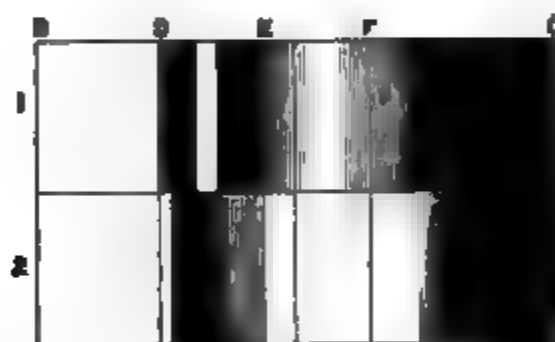
¹ Pflüger, 'Die normalen Gasmenge des arteriellen Blutes nach verbesserten Methoden.' *Centralblatt f. d. med. Wissenschaft*, 1867, No. 46.

² It has been stated (Fernet) that plain serum likewise takes up a certain amount of oxygen, independently of pressure; this result is probably owing to the presence of a slight amount of hæmoglobin in the serum. Pflüger (*Archiv*, vol. i. p. 73.) found 100 vols. of dog's serum to contain the following gases:—

Oxygen	0·2 vols. at 0° C and 1 metre.
Free carbonic acid	26·8 " " "
Combined carbonic acid	7·1 " " "
Nitrogen	1·7 " " "
					<hr/> 35·8 vols.

compound with oxygen, and it likewise possesses the property of combining with some other gases in constant proportions: 1st. of hæmoglobin combines with 1·2—1·3 CC of O (measured at 0° C and 1 metre pressure). The compound which we may designate O-Hæmoglobin is crystallizable and somewhat less soluble than pure hæmoglobin. Its solutions are of a lighter red than those of the latter; they are not dichroic, whereas hæmoglobin, which is free from gases, and which we may term reduced hæmoglobin, appears green when examined in thin layers. Solutions of O-Hæmoglobin exhibit, when examined by means of the spectroscope, two absorption bands situated in the green portion of the spectrum. Solutions of reduced hæmoglobin, on the other hand, exhibit a single, less defined band, which occupies the interval between the two first bands.

FIG. 2.



(1) Spectrum of O-Hæmoglobin, exhibiting two absorption bands between Fraunhofer's lines D and E. (2) Spectrum of reduced hæmoglobin, showing a single broader absorption band (the band shades off more gradually than is shown in the woodcut).

Oxygen can be removed from its combination with hæmoglobin not only by the means formerly referred to, but also readily by the action of many reducing substances, as by ammonium sulphide, by alkaline solutions of ferrous salts, by iron, by nitric oxide. The minimum pressure required for the persistence of the compound of O + Hæmoglobin, viz., the dissociation tension of the oxygen of the blood, is dependent on the temperature, but its absolute value is still unknown.

In addition to oxygen, hæmoglobin can also combine chemically with carbonic oxide (L. Meyer¹), and with nitric oxide (Hermann²) in the same proportions by volume, therefore in the same equivalent proportions. Of these compounds, that with oxygen is the least stable, so that the oxygen may be expelled from its combination with hæmoglobin by carbonic oxide, and the latter, in its turn, by nitric oxide. Even the two latter compounds are to be

¹ Lothar Meyer, 'Ueber die Einwirkung des Kohlenoxydgas auf Blut.' *Zeitschrift für rat. Med.*, 1859, p. 82.

² Ludimar Hermann, 'Ueber die Wirkungen des Stickstoffoxydgas auf das Blut.' *Müller's Archiv*, 1865, p. 469-481.

designated as unstable, seeing that, according to recent investigation (Donders,¹ Zuntz,² Podolinski³) they are also capable of decomposition by physical means; the pressure at which they decompose is, however, much lower than in the case of the oxygen compound. These CO- and NO-compounds are, like the O-compound, not dichroic, and they possess two absorption bands, which in the carbonic oxide compound are somewhat differently situated from those in the other two analogous compounds. When O-Hæmoglobin is decomposed by means of acids, the oxygen is not liberated and cannot be pumped out; it must, therefore, enter into chemical combination with one of the products of decomposition (L. Meyer, Zuntz, Strassburg).

Seeing that the behaviour of the blood as a whole towards oxygen (carbonic oxide, &c.), as well as its optical properties and the dependence of these upon the gas contained in the blood, is exactly the same as that of a solution of hæmoglobin, and, further, as blood when saturated with oxygen takes up almost exactly as much of that gas as corresponds to the amount which its hæmoglobin can combine with, it follows that all the loosely combined oxygen of the blood is linked to hæmoglobin.

[One gramme of hæmoglobin can, according to Preyer's observations, combine with 1.27 CC of oxygen at 0° C and one metre pressure. According to Hoppe-Seyler dog's blood contains on an average 13.79 per cent. of hæmoglobin. The amount of oxygen which this amount of hæmoglobin would hold, if thoroughly saturated with oxygen, would then be $13.79 \times 1.27 = 17.5$ CC. Pflüger actually found that arterial blood of the dog contains on an average 16.9 CC of oxygen gas measured at 0° C and 1 metre pressure.]

The oxygen of the blood is given up so readily to oxidizable substances that it has been thought to be present in the form of 'active oxygen' or 'ozone,' O₃. The following properties of blood appeared to favour this view. 1. Both the blood corpuscles and hæmoglobin are so-called 'ozone-transferrers,' that is, they possess the power of immediately transferring ozone from substances in which it is present (as turpentine which has been kept for a long time) to readily oxidizable substances (ozone reagents, such as tincture of guaiacum, which becomes blue by oxidation, Schoenbein, His); for this reaction the presence or absence of oxygen in the blood is of no importance (for instance, it may be saturated with CO). 2. Blood and hæmoglobin can themselves ozonize oxygen, so that in presence of air they can cause guaiacum tincture to become blue (A. Schmidt⁴); if the blood itself contains oxygen, the presence of air is not necessary; it is necessary if the blood has been saturated with CO (Kühne and Scholz⁵). On the activity of its oxygen depends the decomposition of sulphuretted hydrogen by blood.

[The facts stated above afford no sufficient ground, however, for believing that the oxygen of blood exists in the condition of ozone. They would rather seem to show that oxygen, like other elements, at the moment of its liberation from chemical combination, i.e., when in a *nascent condition*, possesses chemical activities which do not belong to the free gas.

Pflüger has, indeed, expressed the opinion that the most striking of the

¹ F. C. Donders, 'Der Chemismus der Athmung, ein Dissociations-Process.' *Pflüger's Archiv*, v, 20-26.

² N. Zuntz, 'Ist Kohlenoxydhæmoglobin eine feste Verbindung?' *Pflüger's Archiv*, v, 584-588.

³ Podolinski, 'Ueber die Austreibbarkeit des CO und NO aus dem Blute.' *Pflüger's Archiv*, vi, 558.

⁴ Schmidt, 'Ozon im Blut,' Dorpat, 1864; *Archiv f. path. Anat.* Bd. xlii, p. 249.

⁵ Kühne und Scholz, *Archiv. f. path. Anat.* Bd. xxxiii, p. 96.

ozone-like properties of the oxygen of the blood, viz. the blueing of guaiacum, is necessarily associated with a decomposition of hæmoglobin.]

2. *Carbonic acid* is found in arterial blood on an average in the proportion of about 30 vols. per cent. : venous blood from muscles at rest yields about 35 per cent. A portion of the carbonic acid can only be driven out by acids; it is therefore in stable chemical combination. The carbonic acid removable by the pump may either be merely absorbed, or partly in very weak chemical combination. A weak chemical combination may take place either with 1, the carbonate of sodium of the plasma, 2, the phosphate of sodium of the plasma (Fernet¹), 3, through as yet unknown combinations in the blood corpuscles (Pflüger and Zuntz,² Ludwig and A. Schmidt³). Since solutions which contain carbonic acid, either absorbed or in weak combinations, have an acid reaction, the fact that blood has an alkaline reaction would appear opposed to the view that carbonic acid is present in other than a stable combination (Preyer), were it not that blood still gives an alkaline reaction when *saturated* with carbonic acid (Pflüger and Zuntz).

Since the phosphate of sodium in blood ash is derived almost entirely from burnt lecithin, the second combination referred to is probably only very slightly operative (Hoppe-Seyler and Sertoli⁴). Since, moreover, the serum takes up carbonic acid independently of pressure, just like the blood itself, a part, at least, of the chemically combined carbonic acid must be in the serum (that is, in the plasma), probably in the form of sodium bi-carbonate (see above No. 1). That a part of the carbonic acid is combined in the blood corpuscles (see No. 3) is shown by the fact, that blood contains scarcely less carbonic acid than a similar volume of serum (Ludwig and Schmidt), and moreover that the absorption of carbonic acid by blood and by serum under increasing pressure occurs according to different laws (Pflüger and Zuntz).

Carbonate of sodium is changed by the addition of carbonic acid into the bi-carbonate $\text{CO}_3\text{Na}_2 + \text{CO}_2 + \text{H}_2\text{O} = 2 \text{CO}_3\text{NaH}$; the neutral salt is again formed along with free carbonic acid by the employment of the means used to drive out the gases. Neutral phosphate of sodium takes up carbonic acid in a similar manner, one equivalent of acid to two equivalents of salt (Fernet), forming an acid phosphate and neutral carbonate: $2 \text{PO}_4\text{Na}_2\text{H} + \text{CO}_2 + \text{H}_2\text{O} = 2 \text{PO}_4\text{NaH}_2 + \text{CO}_3\text{Na}_2$ (Hermann). The means used to drive off the gases break up these combinations, giving off CO_2 and again forming the neutral salt.

3. Blood contains from 1-2 vols. per cent. of *Nitrogen*. A small portion of this gas also is probably chemically combined, being most likely contained in the blood corpuscles (Fernet, Setschenow).

When heated (Thiry⁵) or merely allowed to stand (Brücke) the blood gives off traces of ammonia, probably arising from the decomposition of some ammoniacal salt contained in the blood (Kühne and Strauch⁶); no proof has, how-

¹ Fernet, 'Du rôle des principaux éléments du sang dans l'absorption ou le dégagement des gaz de la respiration.' *Ann. des Sciences naturelles*. 1857; p. 521.

² Pflüger u. Zuntz, *Pflüger's Archiv*, Bd. i. p. 361.

³ Ludwig u. A. Schmidt, 'Arbeiten aus d. Phys. Anstalt zu Leipzig.' 1868, p. 1-61.

⁴ Sertoli, 'Ueber die Bindung der Kohlensäure im Blute und ihre Ausscheidung in der Lunge.' *Hoppe-Seyler's Untersuchungen*. Heft 3, p. 350, et seq.

⁵ Thiry, *Zeitschrift f. rat. Med.* 3rd Series, vol. xvii, p. 166.

⁶ Kühne u. Strauch, *Centralblatt f. d. med. Wissenschaft*. 1861, p. 561 & 577.

ever, yet been obtained of the presence of such a salt in the blood (Brücke). The addition of oxygen favours the development of ammonia (Exner).

Blood which has been deprived of its gases is very dark (almost black), dichroic, and, in consequence of the destruction of the blood corpuscles, lake-coloured.

Different kinds of Blood.

The composition of the blood is not the same throughout the whole body. The greatest difference is observed between *arterial* blood (viz., that which is contained in the systemic arteries, the left side of the heart, and the pulmonary veins), and *venous* blood (viz., that of systemic veins, the right side of the heart, and the pulmonary arteries), and consists principally in the amount of gases contained, and in the colour. Arterial blood contains more oxygen (on the other hand, less carbonic acid) than venous, and has a brighter (scarlet) colour; it does not display the dichroism of the latter. This difference in colour is closely connected with the difference in the amount of oxygen; for, on shaking up dark-coloured blood with oxygen (or with atmospheric air), it becomes bright red, and bright red blood becomes dark-coloured when shaken with other gases (except carbonic oxide).

Moreover, arterial blood contains more water, fibrin, salts, sugar, and extractive matter than venous, but on the other hand fewer blood corpuscles and less urea. Its temperature is on an average 1° C. lower (Chap. VII.) The changes effected by gases in the colour of the blood probably depend, on the one hand, on an alteration in the shape of the blood corpuscles, which shrink and become more concave in appearance on combination with oxygen, swelling out, on the other hand, on the removal of the oxygen (by the passage through it of carbonic acid, &c.) (Harless). In the first case, the blood corpuscles, acting as more powerful concave mirrors, would reflect light in a more concentrated form, whilst in the latter they would tend more to disperse it. At all events, it is in this manner that the addition of salts to the blood renders it brighter. The addition of water, on the other hand, darkens it. Gases, however, exert an action on the pigment which is quite independent of any alteration which they may bring about in the shape of the corpuscles—an action which may be observed after these bodies have been broken up by the addition of water; in lake-coloured blood, however, the colour being darker of itself, the action of oxygen is less easily seen.

The peculiar composition of particular kinds of blood (the blood of the portal, hepatic, and splenic veins), as well as the influence on the blood of digestion, respiration, &c., will be treated of in later chapters.

The changes taking place in the physical and chemical constituents of the blood, its waste and reparation, form the subject of the sixth chapter.

The Quantity of Blood in the Body.—Its Quantitative Composition.

The quantity of blood contained in the human body is not accurately known: it amounts to about $\frac{1}{13}$ (Bischoff¹) of the whole weight of the adult body; to about $\frac{1}{19}$ (Welcker²) of its weight at birth.

The following are the best known methods for determining the quantity of the blood: 1. By ascertaining the dilution of the blood caused by the injection of a known quantity of water; the degree of dilution is determined by comparing the amount of water contained in two samples of the blood taken, the one immediately before, the other a short time after, the injection of the water (Valentin³). [This gives too high a result, both because the water does not become equally mixed with the whole of the blood, and also because the diluted blood commences at once to diffuse throughout the tissues, giving off water (mainly through the kidneys) and taking up solid matter.] 2. By bleeding freely (by beheading) and washing out the blood still left in the vessels with water (until the latter becomes no longer coloured), the amount of the solids contained in the whole of the blood is determined; the quantity of blood can then be ascertained, by comparing these solids with the amount of solids contained in an undiluted sample of blood (Ed. Weber). [Inaccurate, both because all the blood is never washed out of the vessels, and also because the water flowing through the vessels takes up substances, by diffusion, from the parenchyma.] 3. The blood remaining in the vessels after decapitation is diluted with water until it is identical in colour (when layers of equal thickness are compared), with a measured sample of blood previously obtained, and diluted with a known quantity of water; the quantity of blood is then easily calculated from the amount of water required for dilution (Welcker,⁴ Heidenhain⁵). The amount of hæmoglobin contained in the muscles (Chap. VIII.) must be allowed for. It is advantageous to saturate the blood with carbonic oxide (see above), so as to avoid variations in colour, due to unequal saturation with oxygen (v. Bezold and Gscheidlén).

[Summary of the Quantitative Composition of the Blood.]

1. *Relative proportions of blood corpuscles and plasma.*—We possess much scantier information concerning the actual quantitative composition of the blood of man than of that of some of the lower animals.

In reference to the relative proportions of blood corpuscles and plasma we can, indeed, make no more than a probable estimate; for the older analyses of human blood which (like those of C. Schmidt) endeavoured to ascertain these data, were performed according to methods which are erroneous, and which certainly led to false results. Schmidt, for instance, stated that 1,000 parts in weight of the venous blood of man contain 513·04 parts of blood corpuscles and 486·96 parts of plasma—a result which we may safely pronounce to be erroneous.

¹ Bischoff, *Zeitschrift f. Wiss. Zool.*, vol. vii. p. 331; vol. ix. p. 65.

² Welcker, *Prager Vierteljahrschrift*, vol. iv. p. 11.

³ Valentin, *Canstatt's Jahresbericht*, 1844, p. 169.

⁴ Welcker, *loc. cit.*

⁵ Heidenhain, *Disquisit. crit. et expos. de sang. quantit.* Halis, 1857.

As we are now in possession of a very accurate method of counting the number of blood corpuscles present in a known volume of blood (method of Malassez), and know almost exactly the volume and specific gravity of the human blood corpuscles, we may make a close estimate to the mean relation of corpuscles and plasma in the blood of man. Assuming the number of corpuscles in a cubic millimetre of blood to be 5,000,000, the volume of each corpuscle to be 0·000000072 cubic millimetre, and its density to be 1,105 (Welcker), the following would be the proportion of blood corpuscles and plasma in 1,000 parts of human blood: blood corpuscles 376 parts and plasma 624 parts. In the case of horse's blood, Hoppe-Seyler has determined 1,000 parts of blood to contain 326 parts of corpuscles and 674 parts of plasma.

2. *Chemical composition of organic matters of the corpuscles.*—The composition of the blood corpuscles of man has been ascertained by Jüdel.

In 100 parts of corpuscles there are:—

Water	56·5 parts.
Solids	43·5 „

The dried organic solid matter consists (in 100 parts) of:—

Hæmoglobin	86·8 to 94·3 parts.
Proteid matters	5·1 to 12·2 „
Lecithin	0·3 to 0·7 „
Cholesterin	0·25 parts.

3. *Chemical composition of the plasma.*—The plasma of human blood has been analyzed by Strecker, and the results agree very closely with those obtained by Hoppe-Seyler in horse's blood.

Strecker found in 1,000 parts of plasma:—

Water	903·0 parts.
Fibrin	4·0 „
Albumin of serum	78·8 „
Fats	1·7 „
Extractive matters	3·9 „
Salts	8·6 „

4. *Salts of the blood.*—In reference to the inorganic salts of the plasma and the blood corpuscles, we have the analyses of Carl Schmidt, which have shown that the ash of the blood corpuscles is specially rich in potassium salts, whilst that of the serum abounds in sodium compounds.

<i>In 1,000 parts of Corpuscles.</i>			<i>In 1,000 parts of Plasma.</i>		
Potassium chloride	.	3·679	Potassium chloride	.	0·359
„ sulphate	.	·132	„ sulphate	.	0·281
„ phosphate	.	2·343	Sodium phosphate	.	0·271
Sodium phosphate	.	0·633	Calcium „	.	0·298
Calcium „	.	0·094	Magnesium „	.	0·218
Magnesium „	.	0·060	Soda (?)	.	1·532
Soda (?)	.	0·341	Sodium chloride	.	5·546
		7·282			8·505

5. *Quantitative composition of human blood as a whole.*—The following numbers represent the proportions in which the chief constituents occur in the blood of man; they are to be looked upon as merely approximative.

In 1,000 parts of human blood there are:—

Water	770·0 to 790·0 parts.
Fibrin	2·0 to 2·5 „
Hæmoglobin	125·0 to 140·0 „
Serum—albumin, and other proteids		50·0 to 70·0 „
Salts	6·0 to 8·0 „

Note.—In drawing up this table use has chiefly been made of the results obtained by Becquerel and Rodier, who had much more extensive opportunities of examining the blood of man than has fallen to the lot of more recent investigators. The amount of hæmoglobin is calculated from the determinations of the iron contained in human blood made by these observers, as well as by Gavarret.]

Death of the Blood—Coagulation.

So soon as blood or liquor sanguinis is withdrawn from the influence of the walls of living vessels, it quickly runs through a series of changes, which may be said to attend the death of the blood. They are as follows:

1. *Coagulation*, that is, the separation of a solid albuminous body, 'Fibrin.' The liquid blood is thus changed, in the first place, into a soft red mass; in a few hours, however, the solid portion contracts, pressing out a yellow fluid—the blood serum; the solid portion retains, however, the shape of the vessel containing it, but on a smaller scale. The firm red mass, the *blood clot* (*placenta sanguinis*), now floating in the serum, consists of matted filaments of fibrin, and the blood corpuscles imprisoned within them, together with some occluded serum. The fibrin is separated essentially from the plasma and not from the blood corpuscles; for the former, which may be obtained either by allowing the corpuscles in uncoagulated blood to sink to the bottom, or by filtering blood containing large corpuscles (frog's blood diluted with sugared water, J. Müller¹), undergoes coagulation, forming a white cake which consists solely of fibrin. The serum consequently contains the same component parts as the plasma, with the exception of fibrin. If before coagulation the blood corpuscles have had time to sink (as is usually the case with the blood of the horse), the upper layer of the blood clot consists solely of fibrin, without corpuscles, and is therefore white and of closer texture than the red portion; this is called the 'Buffy Coat' (also 'crusta phlogistica,' from its occurrence in blood obtained by bleeding animals affected with inflammatory diseases). Fibrin may also be obtained by whipping recently drawn and yet uncoagulated blood with twigs,

¹ Müller, 'Beobachtungen zur Analyse der Lymphe des Bluts und des Chylus,' Poggen-dorff's *Annalen*, 1832, vol. xxv. p. 537.

cally, the ferment. Both the fibrin generators are soluble in alkalies and acids and in solutions of common salt; they are soluble in water if a stream of oxygen be passed through it.

The ferment is obtained by adding alcohol to blood, and extracting the thoroughly dried and filtered residue with water. Blood allowed to flow directly from an artery into alcohol yields no ferment.

On mixing solutions of fibrinogen and the fibrinoplastic substance in the presence of the ferment, fibrin separates first as a gelatinous substance, which afterwards contracts; the quantity of these two substances determines the *amount* of fibrin, to form which they appear to combine, although in proportions which are not constant. The amount of ferment present merely influences the *rapidity* of the separation of fibrin. Serum contains an excess of fibrinoplastic substance (that of ox's blood contains 0·7–0·8, of the horse 0·3–0·6 per cent). Presence of non-crystallizable hæmoglobin, of carbon, platinum, &c. hastens the formation of fibrin, when all other conditions are present. If solutions of the fibrin generators and of the ferment are deprived of oxygen, by passing hydrogen through them, before they are mixed, no fibrin is formed (A. Schmidt).

The connection between the above and the other phenomena accompanying the death of the blood, particularly acidification, is unknown. Blood which has undergone these changes, if kept longer, particularly if defibrinated, gradually loses the whole of its oxygen, carbonic acid taking its place: at the same time putrefaction sets in.

The phenomena accompanying its death are the result of the cessation of an influence exercised constantly upon the blood during life, by the living walls of the vessels (Brücke¹). The blood does not coagulate as long as it circulates in the vessels, so that every portion of it constantly comes in contact with their living walls; nor does it coagulate if, after being drawn, it is in contact with a living vessel (as, for instance, when frog's blood is placed, over mercury, in contact with a pulsating frog's heart, Brücke). On the other hand, it coagulates after it has been drawn from the vessels, or in the vessels, after their death, or even in living vessels, if at any point stagnation of the blood occurs, so that the central layers are removed from the influence of the walls.

Many precise accounts concerning the causes of the process of coagulation are here passed over, because they have not been verified. According to our present views of fibrin formation, Brücke's law would be expressed as follows: the influence of the living vascular wall is to hinder the formation of the fibrin ferment, or to destroy it continuously as soon as it is formed.²

All the phenomena which characterize the death of the blood are hastened by high temperatures, and by the contact of the blood with foreign bodies (as by stirring), also by air (blood coagulates more quickly in open vessels than over mercury).

¹ Brücke, *British and Foreign Med. Chir. Review*, 1857, p. 183.

² [The reader who is interested in this subject is advised to study the most suggestive Croonian Lecture by Professor Lister (Proceedings of the Royal Society, 1863), in which he will find many facts which are opposed to Brücke's theory, and which it is difficult to explain even with the light of Schmidt's most recent researches.]

to the protection of the tissues, it dies but slowly in cold-blooded animals, although quickly, in spite of this, in warm-blooded; thus are explained the above-mentioned facts.

The above-described phenomena show that in the process of dying the blood undergoes complex chemical changes. The most striking of these, the coagulation of fibrin, was formerly considered to be a spontaneous coagulation of an albuminous substance dissolved in the plasma. We now know that the fibrin, as such, does not exist in the blood, but originates in the process of dying. According to the ideas most generally received (A. Schmidt¹), it arises from the chemical combination of two albuminous substances, separate, although existing side by side, in the blood—'fibrinogen' and the 'fibrinoplastic substance.' This combination is brought about by a ferment—the '*fibrin-ferment*'—which is only developed during the death of blood. Both the fibrin generators are contained in the plasma.

[Schmidt's most recent researches lead him to believe that the fibrin ferment and the fibrinoplastic substance are the results of death-changes in the colourless corpuscles of the blood and in certain cells which appear to be intermediate between the colourless and coloured corpuscles. Some of the principal grounds upon which this belief are based are—1stly, that when the coagulation of blood plasma is prevented by cold, the more superficial strata from which the colourless corpuscles have subsided coagulate very feebly, whilst the deeper strata which are crowded with colourless corpuscles coagulate strongly; 2ndly, that in the slowly coagulating plasma of horse's blood which has been exposed to cold, a process of breaking down of the colourless and intermediate blood corpuscles appears to be the precursor of actual coagulation.]

The fibrin generators are also contained in many other normal and pathological fluids, *e.g.* in lymph and chyle, in pericardial and hydrocele fluids, &c. The former of these fluids also generate the ferment, and therefore coagulate spontaneously, although more slowly than the blood; the others do not generate the ferment, and therefore coagulate only after the addition of ferment or of blood. Fibrinogen and the fibrinoplastic substance are most closely related to globulin. They can be obtained from their natural solutions in blood-plasma by the addition of water and the subsequent passage of carbonic acid; the fibrinoplastic substance is first precipitated and carries down with it, mechani-

¹ A. Schmidt, 'Ueber den Faserstoff und die Ursachen seiner Gerinnung,' *Müller's Archiv*, 1861, pp. 545-587, and 675-721; 'Weiteres über den Faserstoff und die Ursachen seiner Gerinnung,' *Müller's Archiv*, 1862, pp. 428-469, and 533-564; 'Neue Untersuchungen über die Faserstoffgerinnung,' *Pflüger's Archiv*, vol. vi. (1872), pp. 413-538; 'Ueber die Beziehungen des Faserstoffes zu den farblosen und den rothen Blutkörperchen und über die Entstehung der letzteren' (vorläufige Mittheilung von Prof. Alex. Schmidt in Dorpat), *Pflüger's Archiv*, vol. ix. (1874), pp. 353-357; 'Ueber die Beziehung der Faserstoffgerinnung zu den körperlichen Elementen des Blutes,' 1. Theil. 'Der Faserstoffgerinnung,' *Pflüger's Archiv*, vol. xi. (1875), pp. 291-369; 'Ueber die Beziehung der Faserstoffgerinnung zu den körperlichen Elementen des Blutes,' 2 Theil vol. i. (1875), pp. 515-577; 'Ueber die Beziehung des Kochsalzes zu einigen thierischen Fermentationsprocessen,' *Pflüger's Archiv*, vol. xiii. (1876), pp. 93-146; 'Bemerkungen zu Olof Hammarstan's Abhandlung,' 'Untersuchungen über die Faserstoffgerinnung,' *Pflüger's Archiv*, vol. xiii. (1876), pp. 146-176.

capillaries to the systemic, the blood is rich in oxygen, and consequently *bright red* or *arterial*; on the other hand, during its passage from the systemic to the pulmonic capillaries, it is poor in oxygen, but rich in carbonic acid, and therefore *dark red* or *venous*. The whole circulation, therefore, naturally divides itself into two halves, an arterial and a venous.

At the commencement of each of the trunks of the vascular system (the one the arterial, the other the venous) is placed the principal motor apparatus, in the form of two contractile pouches, supplied with valves—the two halves of the heart—the left being on the arterial side of the circulation (commencement of the aorta), the right on the venous (commencement of the pulmonary artery). Reckoning from the heart forwards, all those vessels which carry blood *to* a capillary system are called arteries, whilst those carrying the blood *from* a capillary system are called veins. There are therefore two arterial and two venous systems. The systemic arterial system (the aortic system) carries arterial blood from the left side of the heart into the systemic capillaries; the systemic venous system carries this blood, now become venous, into the right side of the heart, from which the pulmonary arterial system carries the venous blood into the pulmonary capillaries, and the pulmonic venous system returns this blood, again become arterial, into the left side of the heart.

Although the complete circulation forms one single circuit, the course of the blood from the left side of the heart through the systemic capillaries to the right side of the heart is often erroneously described as the greater or systemic circulation, the other as the lesser or pulmonary circulation. One portion of the systemic venous blood, viz. that coming from the capillaries of the intestines and spleen, unites to form one vein (the portal vein), which does not proceed directly to the right side of the heart, but branches out, like an artery, into a second capillary system in the liver, whence it passes into veins leading direct to the heart. This section of the vascular system is erroneously called the portal circulation.

Since the sum of the diameters of the branches of an artery almost always exceeds the diameter of the trunk, the sum of the diameters of the vascular system must in general increase with its ramifications, and consequently is smallest in the two trunks (the aorta and pulmonary artery), and greatest in the capillaries. The vessels, especially the arteries, are very elastic.

Amongst the motive powers producing the circulation of the blood the movements of the heart occupy the first place. The description of the circulation as a whole will therefore be preceded by an account of the most essential facts relating to the heart.

The Movements of the Heart.

The heart consists of two hollow muscular organs, completely divided, though of similar construction; each of these transmits its contents in a definite direction by means of rhythmical contractions and valvular arrangements. The right half of the heart is connected with the venous, the left with the arterial half of the circulation; the former therefore contains only dark red, the latter only bright red blood;—the former transmits, through the pulmonary artery, the blood pouring into it through the *venæ cavæ*, the latter transmits through the aorta the blood brought back from the lungs by the pulmonary veins. Each half of the heart consists of a thin-walled antechamber (auricle, atrium), which first receives the entering blood, and a thick-walled chamber (ventricle), which forces it into the artery.

Although entirely removed from the control of the will, the muscular fibres which form the greater portion of the walls of the heart are transversely striated; they differ, however, from almost all other transversely striated muscular fibres, as they ramify and join together. They form numerous layers diversely arranged—partially in spirals. Those of the ventricles spring from the fibro-cartilaginous rings at the margins of the auriculo-ventricular openings, and, in part, return to be inserted in the same, while, in part, they are inserted in the *chordæ tendinæ*, after forming the *musculi papillares*. The muscles of the auricles are entirely distinct from those of the ventricles, but many fibres pass from the right side of the heart to the left. This arrangement of the muscles explains why both auricles or both ventricles always contract simultaneously, whilst the movements of the auricles and ventricles are independent of each other.

The heart in mammals and birds resembles the human heart. In scaly amphibia the two ventricles communicate; in the naked amphibia only one is usually present. In the former the aorta and pulmonary artery originate from the common ventricular cavity, in the latter only one vessel leaves the ventricle, supplying blood both to the body and the lungs. In fishes and in undeveloped batrachians the heart usually corresponds to the right half only of the human heart (one ventricle and one auricle); no heart is inserted in the arterial half of the circulation, so that the branchial veins open directly into the aorta. In invertebrata, which usually possess no closed vascular system, a real heart with auricles and ventricles exists only in a few orders; in some there exists merely an open bag provided with valves (as the dorsal vessel of insects); others have no such apparatus.

The rhythmical movements of the heart consist of an alternate contraction of the auricles and ventricles. The two halves of the heart work in all respects correspondingly and simultaneously. During the contraction (systole) of the two auricles, the dilatation (diastole) of the ventricles takes place, and conversely. The systole of the ventricles directly follows that of the auricles; on the other hand, a slight pause occurs after the systole of the ventricles before the following systole of the auricles; the systole of the auricles, moreover, lasts a shorter time than that of the ventricles.

The systole of the ventricles takes up about two-fifths, their diastole about three-fifths of a complete cardiac revolution (Valentin, Landois¹). This, how-

¹ Landois, *Centralblatt f. d. med. Wissenschaft.* 1866, p. 177.

ever, is only when the pulse is of normal frequency, since any change in its rate only varies the duration of the diastole, whilst that of the systole remains constant.

[It was found by Donders¹ in a large number of observations, that whilst the duration of a complete cardiac revolution varied between 0·640'' and 0·806'', the duration of ventricular systole fluctuated within very narrow limits, viz., between 0·301'' and 0·327''].]

The heart and large vessels lie within the thorax, in a spacious, closed chamber, which, together with the lungs, they tend to fill; in doing so they are dilated beyond their natural volume (see Chapter IV.); they are, therefore, under negative pressure, *i.e.* their walls (more especially those of the auricles and of the large veins which are most yielding) are drawn apart. The relaxed heart, therefore, tends to distend itself by sucking blood out of the veins. Owing to a special contrivance, the aspiration of blood *through* the veins is not even interrupted during the contraction of the ventricle—which must be looked upon as the heart-pump proper—but proceeds continuously.

As the large veins open into the contractile auricles they possess a varying capacity. During the ventricular systole the auricles are relaxed, and are therefore in a position to receive the blood which is, in the meantime, sucked up into the thorax. During the diastole of the ventricles, on the other hand, blood flows into them from the then contracting auricles, without the passage of blood through the veins into the auricles being interrupted. The auricle must therefore not be considered as a preliminary suction- and force-pump, whose action is followed by that of a second pump, the ventricle, but is to be looked upon merely as a reservoir which regulates the pressure of blood in the venous system. Each lateral half of the heart, therefore, being a simple suction- and force-pump, merely requires a valvular arrangement at its orifice of entrance and exit; the first is formed by the auriculo-ventricular, the second by the semilunar valves. During the systole of the auricles the blood is sucked into the synchronously relaxed ventricle by the aspiration of the thorax (aided, perhaps, by the active power of aspiration exerted by the ventricle in its diastole, and to which we shall afterwards refer), so that no valves are required to prevent its reflux into the venous trunks. It is only the coronary veins which empty themselves into the right auricle, and whose contents being regulated, not by atmospheric, but by intra-thoracic pressure, require a valvular arrangement, and this is provided for by the so-called *valvula Thebesii*.

The auricular cavities are never completely obliterated during contraction, though this appears to be the case with the auricular appendages.

¹ Donders, *De Rhythmus der Hartstoonen*. *Nederlandsch. Archief voor Genees- en Natuurkunde*, 1865, p. 139. Translated in full by Dr. Moore in *Dub. Quart. Journ. of Med. Sc.* vol. xlv. p. 225.

The action of the heart as a pump commences with the systole of the ventricles, which changes the negative pressure of the contents into a positive pressure, and causes the auriculo-ventricular valves to close. The closure of the valves is furthered by the simultaneous contraction of the *musculi papillares*, whilst the contraction of the ventricles forces their whole contents, with great energy, into the arteries (aorta and pulmonary artery). As soon as the systole ceases, the high pressure of the blood in the large arteries closes the semilunar valves, so that a reflux of blood into the relaxed ventricle is impossible. After a short pause, during which, as was previously mentioned, the ventricles receive blood from the previously filled auricles, the action recommences with the auricular systole.

The auriculo-ventricular valves, viz., the tricuspid on the right and the mitral on the left side of the heart, consist respectively of three and two segments, which are connected by a broad basis to the walls of the auriculo-ventricular openings, whilst their free margins are connected to the *musculi papillares* by means of the *chordæ tendineæ*. When not in action these valves hang slackly in the ventricles. As soon as the pressure within the ventricle surpasses that in the auricle, the back current drives them up, causes them to unfold, and as they are prevented by the *chordæ tendineæ* from passing into the auricle, their inner borders are pressed together, so that a complete closure is effected.

The semilunar valves are formed by three pocket-like membranes situated at the commencement of the aorta and pulmonary artery. These pouches oppose no obstacle to the passage of blood into the arteries, but so soon as the pressure in the latter becomes greater than that in the ventricles, they fall together, and by their edges press against one another. Their edges then form a three-pointed star. In this position the semilunar valves form a strong barrier between the ventricle and artery.

The position of the semilunar valves during systole, and their relation to the coronary arteries, which take their origin in the sinuses of Valsalva, at the commencement of the aorta, are subjects of dispute. Some (Scaramuzzi, Thebesius, Brücke¹) suppose that during systole the valves lie close to the arterial wall, in such a manner as to close the openings of the coronary arteries, so that the latter are only supplied with blood during diastole. The result of this would be a more easy entrance of blood into the substance of the heart during its relaxation, and a distension of the ventricle in diastole, due to a turgescence of its walls, whereby an active *aspiration* of the blood streaming out of the auricle would be effected ('Selbststeuerung des Herzens' of Brücke).

Others (Hamberger, Hyrtl,² Rüdinger,³ Oehl, Ceradini⁴) raise the following objections to this view. (1.) The valves are not pressed against the wall during systole, but are stretched across and away from the sinuses. (2.) When the coronary arteries are cut across, blood flows from them, specially during systole, and from their central ends. (3.) Blood meets with less resistance in flowing through the capillaries of muscles during contraction than relaxation (compare Chapter VIII.) (4.) The capacity of the cavities of the heart is not only not increased by injection of the coronary arteries, but diminished. According to the most recent researches (Ceradini), the diastolic closure of the semilunar valves is not brought about by a regurgitation of blood, but by the elastic rebound of the aortic walls at the time when the systolic stream through the axis of the aorta is interrupted; for, during the passage of blood through the aorta,

¹ Brücke, *Versch'uss der Kranzsch'agadern durch d. Aortenklappen*. Wien, 1855.

² Hyrtl, *Ueber d. Selbststeuerung d. Herzens*. Wien, 1855.

³ Rüdinger, *Beiträge zur Mechan. d. Aortenklappen*. Erlangen, 1857.

⁴ Ceradini, *Der Mechanismus der halbmondförmigen Herzklappen*. Leipzig, 1872

the pressure of blood at the sides of the aorta is greater than in the rapidly moving axial layers.

The shape of the relaxed heart, or more accurately, of the two ventricles, is that of an oblique cone, whose base (a section through the auricular ventricular openings) is an ellipse. By the systole of the ventricles the shape of the heart is altered in such a manner that the base becomes rounded, and the formerly oblique axis vertical, so that an upright cone is formed. The change in form is accompanied by a rotation of the axis, and (owing to the position of the heart in the thorax) a tilting up of its apex, which, in consequence, strikes against the wall of the chest (Ludwig¹). The striking of the cardiac apex against the thoracic wall may also be caused by the so-called *recoil* which is communicated in a reverse direction to every moveable body out of which a fluid is pouring (Gutbrod, Skoda²). Both causes have been supposed to account for the cardiac impulse or apex beat, which may be seen and felt between the fifth and sixth left ribs, a little to the inside of a vertical line drawn through the nipple. When the heart strikes exactly on a rib, only a slight quivering is noticed.

The Sounds of the Heart.—Over the exposed heart, or when the ear is applied directly, or with a stethoscope, to the præcardial region, two sounds may be heard, following in quick succession—the heart sounds. The first (systolic) is a dull sound, loudest in the vicinity of the ventricles, and lasts as long as their systole continues. Some attribute this sound to the vibration of the tense membranous auriculo-ventricular valves, whilst others suppose it to be the *muscular noise* of the contracting heart (Chap. VIII.) That the noise of muscular contraction takes a part in the production of the first sound is known by the fact that it may be heard in a heart which has been cut out and is empty of blood (Ludwig and Dogiel³).

[We may with confidence admit that the causes of the first sound are certainly two, viz. (1) the impact of blood against the closed auriculo-ventricular valves, and (2) the contraction of the muscular substance of the heart; and to these two some have added a third, but certainly much less important factor, viz. the impact of the apex against the thoracic wall.

The contraction of the heart is the only example of a ‘simple muscular contraction’ occurring in the living healthy body. The evidence upon which this statement is based is the following:—If the leg of a recently killed frog be taken, and the yet highly irritable sciatic nerve be made to touch both the auricular and ventricular surfaces of the heart, a simple muscular contraction

¹ Ludwig, *Zeitschrift f. rat. Med.* Bd. vii. p. 189.

² Skoda, *Auscultat. u. Percuss.* 2te Aufl. Wien, 1842, p. 147.

³ Ludwig und Dogiel, ‘Ein neuer Versuch über dem ersten Herzton.’ *Bericht d. k. sächs. Ges. d. Wissenschaft*, 1868, p. 89; Ludwig’s *Arbeiten*, &c., 1868, p. 78.

of the frog's leg follows each systole of the heart. As this result occurs constantly (providing the tissues of the frog be sufficiently irritable), *i.e.* as *tetanic* contraction is *never* induced, this proof afforded by the so-called *rheoscopic frog* is believed to be conclusive. There is a difficulty in the way of admitting the contraction of the heart to be 'simple,' which must, however, be stated. A muscle when performing a simple muscular contraction does not emit a distinct note, the muscular noise being produced by a succession of contractions following one another about twenty times per second. How then does the heart muscle emit a note during contraction? The question yet remains unanswered.]

The second, diastolic, sound follows immediately, and therefore occurs at the commencement of the ventricular diastole. It is shorter and clearer than the first sound, and is caused by the sudden closure of the aortic and pulmonary semi-lunar valves, the *competence* of which is necessary to its production (Williams¹).

The cardiac impulse may be made to register directly the movements of the heart. For this purpose an air-tight drum is placed against the chest wall, and the vibrations of the air contained in it are propagated by a suitable arrangement to a writing lever, which registers them upon a travelling band of paper ('Cardiograph' of Marey). The arterial pulse serves for the indirect registration of the heart's action (see Kymograph, Sphygmograph).

[*The Cardiograph*.—The principle upon which the cardiograph is constructed will be understood by referring to fig. 3, which represents one modification of the original cardiograph of Marey. A is the cardiograph proper; it is a very shallow metallic cup, over the upper part of which a sheet of caoutchouc has been stretched and then fastened air-tight. The cup A has attached to it a short metallic tube, over which a narrow elastic tube can easily be slipped so as to connect it with the apparatus B.

To the centre of the caoutchouc surface *a* is fixed a light metallic disk *b*. *c* is a bent spring, into which fits a screw bearing the ivory or vulcanite knob *d*. By altering the screw, one end of it can be made exactly to touch the metallic disk *b*; any pressure applied to the knob *d* will then cause a depression of the elastic membrane *a*.

B may be termed the recording *tambour*. It is a metallic cup, over the upper surface of which caoutchouc is stretched, and which, like the cardiograph, has a metallic tube leading from it, by means of which it can be connected with the cardiograph. To the elastic upper surface of the *tambour* is fixed a metallic disk, the centre of which bears the fulcrum of the light wooden lever *c*, which carries at its free extremity a light metallic or quill point.

The cardiograph and the tambour being connected, it is obvious

¹ Williams, *Pathology and Diagnosis of the Diseases of the Chest*, 4th edit., 1840; *Report of the British Association*, 1837.

that any pressure exerted on the button *d* of the former will be communicated to the elastic membrane against which it presses, and that air being forced through the tube *f* into the tambour *B*, will cause the membrane of the latter to bulge, and will naturally cause the wooden lever *c* to rise. The movements of the latter will therefore indicate the time at which, and within certain limits, the relative amount of pressure applied to the knob *b*. A graphic record of the movements of the lever *c* may be obtained by causing its point to press lightly against the surface of a revolving cylinder covered with smoked paper.

If the knob *d* be then applied to the part of the thoracic wall where the cardiac impulse is most distinctly seen and felt, a tracing

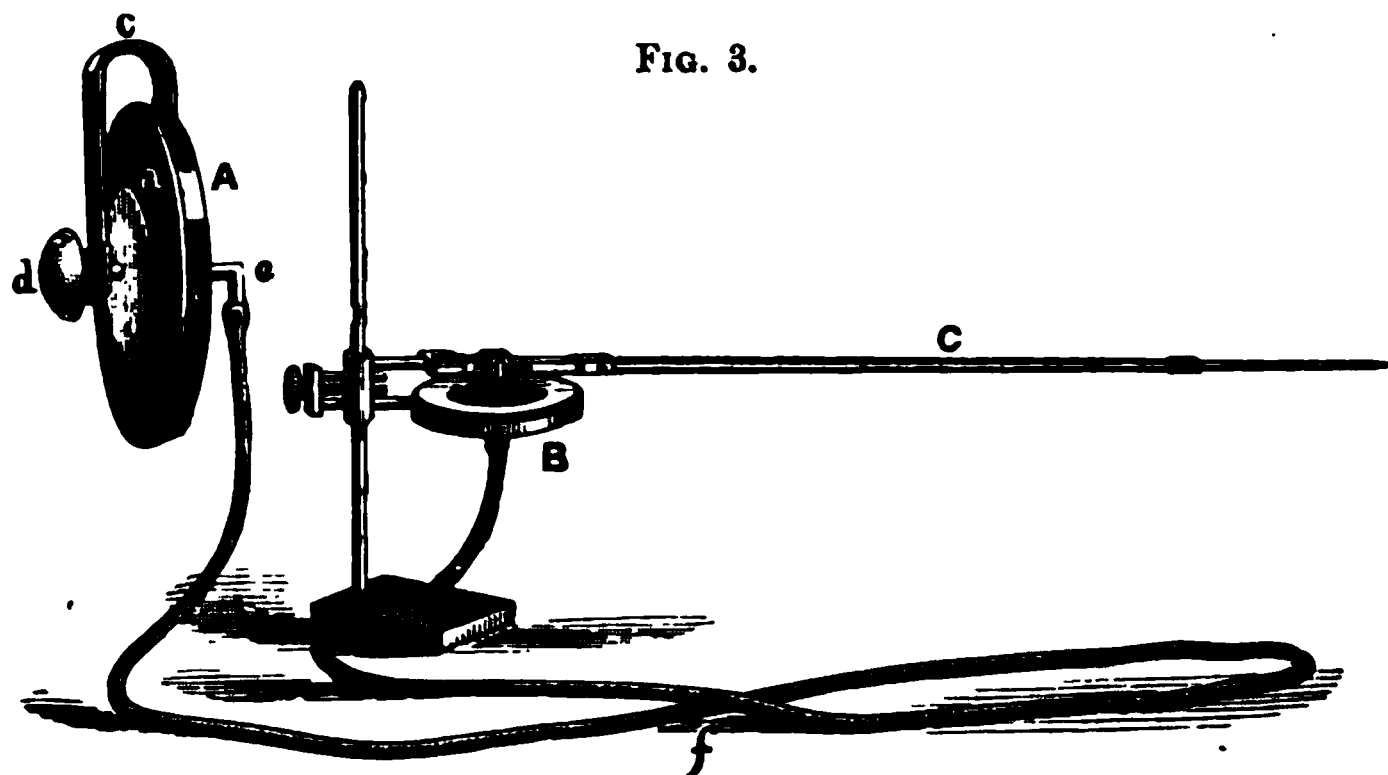


FIG. 3.

SCHEMA OF THE CARDIOGRAPH.

A, cardiograph, connected by means of the tube *f* with
B, recording tambour.

will be obtained which, in particularly favourable cases, presents the chief features of the lowest of the three tracings in fig. 4.

These three tracings were obtained by Chauveau and Marey in an experiment on the horse. A small elastic bag, connected with a tambour similar to that shown in fig. 3, was passed through the jugular vein into the right auricle of the heart of a living horse, and another bag connected with another tambour was passed into the right ventricle; whilst a cardiograph was applied to the chest wall, where the cardiac impulse was most perceptible. The points of the three levers of the three tambours were then placed, exactly one above the other, in contact with a smoked rotating disk; the three tracings were then obtained, of which the upper (marked A) indicates the increase of pressure within the auricle corresponding to contraction of the auricle; the middle (marked v) that of the ventricle, and the lowest (marked c) the cardiac impulse. It will be seen that at the time of auricular systole, indicated by the first high curve in the upper tracing, there is a faint but yet perceptible rise in lowest line traced by the lever of the cardio-

graph-tambour. This, however, commences to rise in a remarkable manner at *sv*, where the dotted ordinate cuts the line, and an irregular curve of considerable extent is traced; this curve, in the

FIG. 4.



TRACINGS OF THE AURICULAR AND VENTRICULAR ENDOCARDIAL PRESSURE, WITH SIMULTANEOUS CARDIOGRAPH TRACING (MAREY).

- A (highest line) indicates the changes in pressure in the auricle. The line is marked by one abrupt curve caused by the auricular systole.
 v (middle line) indicates the changes in pressure in the ventricle.
 c (lowest line) indicates the tracing of the cardiac impulse obtained by means of the cardiograph. The first dotted ordinate, *AS*, cuts the sinuous line at the time when auricular systole commences. The second dotted ordinate, *SV*, cuts it when ventricular systole commences.

cardiograph tracing, is observed to coincide with that in the second tracing, which is caused by the ventricular systole.]

Movement of the Blood in the Vessels.

Causes.

If we imagine the vascular system filled with blood, but with every impulse to motion absent, the blood will stand everywhere within it under equal pressure, which, however, is greater than would be caused by its own weight—a proof that the volume of the blood is greater than the natural capacity of the vascular system (Brunner¹). If in such a system the pressure be suddenly made unequal in two places, a current will be immediately set up

¹ Brunner, *Die mittlere Spannung im Gefäßsystem*. Zürich, 1864.

from the point of greater to that of less pressure. The less the opposition to this adjustment of pressure, the more rapidly does it take place, and the greater, consequently, the speed of the current. At any given moment during this process of adjustment the difference of pressure still remaining must be greater the greater the resistance. It is moreover easy to see that, other things being equal, the speed of the current will increase with the difference in pressure. A constant inequality of pressure is caused in the different portions of the vascular system by the movements of the heart, which thus produce the circulation of the blood.

Imagining the system to have been at rest, the first systole would press a certain quantity of blood (the contents of the left ventricle, see below), just removed from the venous system,¹ into the elastic arterial system, thus raising the pressure in the same. This increased pressure would immediately equalise itself, through the capillaries, with the diminished pressure in the venous system, if the blood did not meet with sensible resistance by friction² against the walls of the smaller vessels, particularly of the capillaries; this so delays the passage through the capillaries that the second systole follows before the adjustment is completed, causing an increased pressure in the arterial system. The same occurs at each succeeding systole, the repletion of the arterial system, and, at the same time, the pressure of the blood from the dilatation of the elastic arterial walls, thus becoming greater and greater. The increasing difference of pressure, however, tends to drive the blood more and more quickly through the capillaries, and it becomes at last so great that as much blood is pressed through the capillaries during the period between two systoles as each systole pours into the arterial system. Under these circumstances no increase of pressure can take place; the difference in pressure now existing between the arterial and venous systems is a *constant* one; it causes a continuous stream through the capillaries, carrying through them just so much blood as the heart rhythmically empties into the arteries. The rhythmic transfer from the venous into the arterial system is thus converted into a continuous current from the arterial into the venous system, through the capillaries (E. H. Weber).³

¹ For the purposes of the following explanation, the right auricle is considered as opening into the left ventricle, the pulmonary circulation, including the right ventricle and left auricle, being left out of the question.

² The resistance to a fluid running through a tube, provided that, like water or blood, it adheres to (wets) the wall, is not caused by the friction against the wall, but by the so-called 'internal friction.' The outer layer of such a fluid remains entirely without motion. If we imagine the whole mass to consist of very thin concentric layers, that layer which is next to the immovable one must rub against it, and so the others, each against the one immediately outside. Every such contact causes resistance by friction ('internal friction'), and thus consumes a portion of the motive power—that is, converts it into heat; each layer is consequently delayed in its course, and the outer ones must naturally be the most delayed, the inner, therefore, the least: consequently the speed is greatest at the axis. It follows that the delay of the axial layer will be greater in narrow than in wide tubes.

³ E. H. Weber, *Ber. d. k. sächs. Ges. d. Wissenschaft. Math. phys. Cl.*, 1850, p. 164; *Archiv. f. Anat. u. Phys.*, 1851, p. 497; 1853, p. 156.

TENSION OF THE VASCULAR SYSTEM.

The contents of the left ventricle, that is, the quantity of blood pumped out during one systole, has been calculated variously at from 150 to 190 grammes. The following are the principal methods: 1. (Legallois, Colin.) The contents of the ventricle may be directly measured by filling the ventricle, before rigor mortis sets in, with a fluid of known specific gravity, and weighing before and after: in this case, as it is impossible to imitate the normal pressure of the heart, the result is valueless. 2. (Volkmann.¹) The diameter of the aorta, and the speed of the current of blood within it, are used to calculate how high a column of blood the heart expels during a unit of time; knowing the frequency of the pulse, the quantity emptied during each systole is found to be about $\frac{1}{400}$ of the weight of the body; that is, in a body weighing 75 kgrms. = 187.5 grms. 3. (Vierordt.²) Given the speed of the blood in any section of the arterial system, the area of that section, and also the area of the aorta, the mean speed in the latter can be calculated, and also the quantity of blood discharged from the left ventricle during a unit of time, since the speed in any two sections is in inverse relation to their contents. The quantity of blood which the right ventricle drives into the pulmonary arterial system must be very nearly the same as that expelled by the left, because the same quantity of blood flows through every section of the vascular system during the same time (see below), and both sides of the heart contract synchronously.

The distension of the arteries and the slackness of the veins show in the simplest manner how much higher is the tension (blood pressure) in the arterial than in the venous system; this is also shown by the height of the jet of blood issuing from an open vessel; from a vein this is seldom of a notable height, whilst the blood from an artery, on the other hand, spurts to the height of several feet.

Absolute determinations of the pressure of the blood may be made by connecting the vessel laterally with a manometer: or the blood itself may be employed as the manometric fluid, by letting it rise in a vertical tube, and measuring the height of the column (Hales³). It is much more advantageous, however, to use the mercurial manometer (Poiseuille⁴) as an 'hæmatodynamometer,' placing a solution of sodium bicarbonate between the blood and the mercury to prevent coagulation. *A priori*, it follows that the blood pressure (that is, the *mean pressure*, apart from the fluctuations of the pulse wave) at one and the same spot of the arterial system will increase:

1. With the fulness of the vascular system, that is, with the quantity of blood.

2. With the frequency and force of the contractions of the heart, for the greater the quantity of blood pumped by the heart from the veins into the arteries, the greater—as is shown above—

¹ Volkmann, *Die Hæmodynamik nach Versuchen*, p. 206, Leipzig, 1850.

² Vierordt, *Die Erscheinungen und Gesetze der Stromgeschwindigkeiten des Blutes*, p. 103, Frankfurt, 1858.

³ *Statical Essays, containing Hæmstatics, or an Account of some Hydraulic and Hydrostatical Experiments made on the Blood and Bloodvessels of Animals, &c.* By Stephen Hales, D.D., F.R.S., Rector of Farringdon. 2nd edition, London, 1740.

⁴ Poiseuille, *J. L. M.*, 'Recherches sur la force du cœur aortique.' Paris, 1826.

will be the constant difference in tension between the venous and the arterial systems.

[3. With the resistance which has to be overcome in forcing the blood from the arteries into the veins. This resistance is conditioned chiefly by the state of contraction or dilatation of the smaller arteries. When these are relaxed, the amount of blood which finds its way from the arteries into the veins between successive systoles is much greater than when they are relaxed; the arteries, therefore, become less distended, i.e. the arterial pressure falls. On the other hand, when the small arteries are contracted the arterial pressure rises and the venous falls. Of the three factors now under discussion, the third is the one which undoubtedly exerts the greatest influence in leading to rapid changes of the arterial pressure.]

The tension, moreover, must vary in different parts of the arterial system. Since any opposition hinders the equalising of the difference in tension, the resistance offered in any one portion of artery by the friction against its walls has an influence on the tension of that particular portion of the arterial system similar to that of the capillaries on the general tension of the arterial and venous systems. The tension must always be greater before any point of opposition than after it has been passed. It follows, therefore, that the blood pressure in the arterial system gradually diminishes from the left ventricle to the capillaries; that the diminution is most rapid where there is the greatest resistance, that is, where contractions occur, and where branches are given off from the trunk, especially if at considerable angles; and that, lastly, the pressure in the principal arterial trunks, on account of their size and the small number of their branches, remains very nearly identical with that of the bulbus aortæ, whilst it diminishes in the smaller arteries (H. Jacobson). Finally, on account of the less resistance offered by the capillaries of the lungs as compared with the capillaries of the body, the difference in tension between the pulmonary arteries and veins will be less, and the pressure in the pulmonary arteries will therefore also be less, than in the systemic arteries, since the quantity of blood rhythmically pumped over is the same in each.

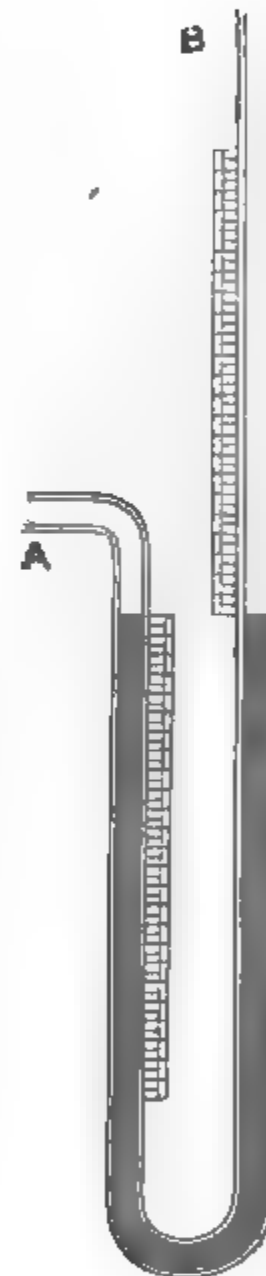
[Methods of determining the Blood Pressure in Arteries and Veins.]

As has been already said, Hales determined the pressure exerted by the blood upon the walls of the arteries and veins through which it flowed, by tying a glass tube into the blood-vessel, and observing to what height the blood rose. Naturally, the blood would continue to rise in the tube until the column of

blood in it exactly counterbalanced the pressure within the blood-vessel. Owing to the comparatively low specific gravity of the blood, the height of this column was in the case of arteries inconveniently high; the blood rising in a tube communicating with the crural artery of a horse above eight feet high. To avoid the inconveniences attending the method employed by Hales, Poiseuille made use of a mercurial gauge or manometer for the determination of the blood pressure, applying to it the term 'hæmatodynamometer.' This instrument consisted essentially of a U-shaped glass tube (fig. 5), the two limbs of which were furnished with a divided scale. Into the U-shaped tube was poured mercury. The bent limb *A* was connected with the blood-vessel in which the blood pressure had to be determined by means of an intermediate tube and a cannula filled with solution of sodium carbonate so as to prevent coagulation of any blood which entered. The upright tube was open. As long as the pressure in *A* and *B* in such an instrument is the same, the mercury obviously stands at the same level in both tubes; an increase of pressure in *A* will cause the mercury to fall in limb *A* and to rise in limb *B*. Now if the scales attached to the two limbs be divided into the same units of length, and if the zero correspond with the level of the mercury in the two tubes when the pressure is equal, then any difference in pressure may be ascertained and estimated in units of the scale (millimetres or inches) by adding together the readings on the two scales, or simply by reading the height to which the mercury has risen in limb *A* above the zero, and then multiplying by two.

Although the mean value of the blood pressure does not usually vary remarkably within very brief intervals of time, yet the blood pressure in arteries does undergo rhythmical variations which correspond: (1) With each systole of the left ventricle; and (2) with each act of respiration; and these are sufficient to keep the mercury in the manometer in a perpetual state of oscillation, individual oscillations following one another so rapidly as to render it very difficult or even impossible to observe them with the naked eye. In order to render it possible to observe carefully the mean blood pressure and the changes which it is continually undergoing, Ludwig modified the hæmatodynamometer so as to cause it to record the movements of the mercury

FIG. 5.

DIAGRAM OF MERCURIAL
GAUGE.

upon a travelling sheet of paper. To this instrument the name of Kymographion (wave-recorder) has been given. One of the many forms of this instrument is shown in the annexed fig. 6.

In the drawing, A represents the mercurial gauge containing mercury; the shorter limb has attached at right angles to it a glass tube, to which is connected a flexible (usually leaden) tube *a*, which terminates in a metallic or glass cannula, which can be introduced

FIG. 6.



MERCURIAL KYMOGRAPHION.

- A is the mercurial gauge.
- B is a cylinder which is driven by clockwork.
- c is the free limb of the mercurial manometer, containing the ebonite float *c d*.
- d is the writing point of the ebonite float.
- e line of 'no pressure' traced by the writing point.
- f curve indicating the fluctuations in the arterial pressure: the large curves correspond with the respirations, the small ones with the contractions of the left ventricle.
- b elastic tube connecting the mercurial manometer with a reservoir of solution of sodium bicarbonate.
- a flexible tube with arterial cannula attached.

into an artery or vein. The shorter limb is continued up for a short distance above the T-piece to which *a* is attached, and is connected by means of an elastic tube *b* with a reservoir containing solution of bicarbonate of soda; the elastic tube may be opened or shut by means of the clamp shown below the letter *b*.

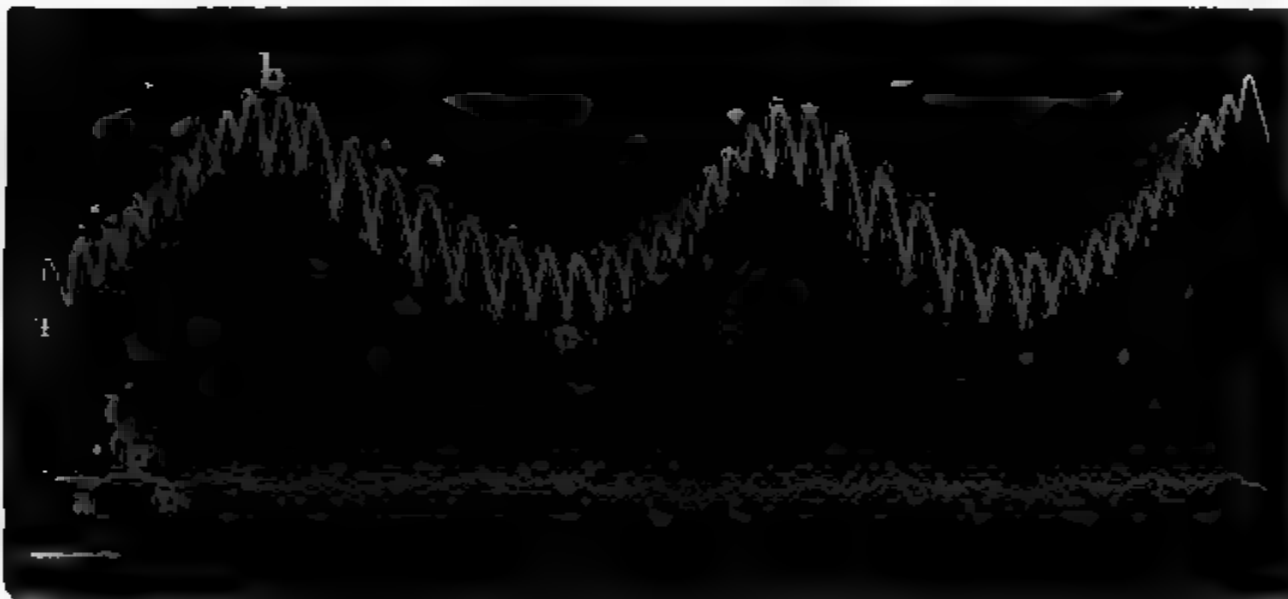
On the surface of the mercury in the longer limb *c* there floats a light ebonite float *c d*; to this float there is attached a light

camel's-hair pencil moistened with ink. This pen is made to press gently against a surface of paper wound round the cylinder *B*, which can be made to rotate at a uniform rate of speed.

By opening the clamp placed on the flexible tube *b*, it is easy to fill the upper part of the short limb of *A* and the tube *a* with solution of sodium bicarbonate, after which the clamp is shut. As the upper part of the short limb *A* now contains a short column of solution of bicarbonate of soda, this will cause the mercury to rise slightly in tube *c*, and accordingly the float will rise and will carry with it the writing point *d*. The latter being pressed gently against the paper covering the cylinder, a horizontal unbroken line represented by *e* is traced; it is traced by the pen at a time when both *a* and *c* are open.

The end of *a* being now closed, the clamp *b* is opened, and solution of sodium bicarbonate is allowed to flow into *A* until the dif-

FIG. 7.



TRACINGS OF THE VARIATIONS IN THE ARTERIAL PRESSURE, TAKEN WITH THE MERCURIAL KYMOGRAPH.

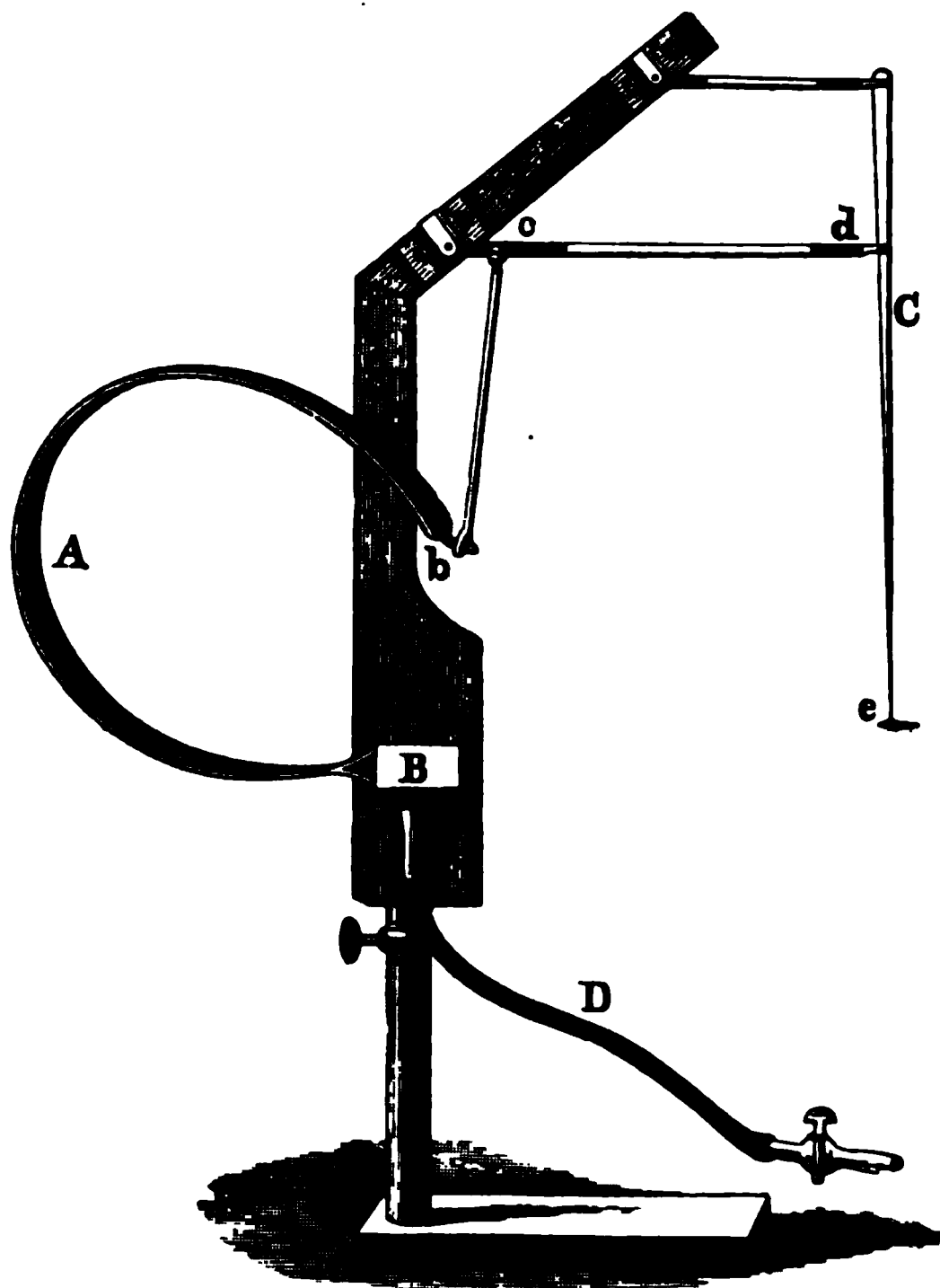
(The upper is from the carotid artery of a dog, the lower from that of a rabbit.)

ference in the height of the mercury in the two limbs is about equal to the estimated blood pressure; the cannula attached to *a* is now introduced into the artery or vein. Let us assume that an artery is chosen. That vessel having been exposed, a ligature is applied to the distal end of the exposed part, and a spring clamp to the proximal. An incision having been made into the intermediate part, the cannula is introduced and then tied in. The clamp on the proximal, cardiac, end is now removed; at once the mercury in the free limb of the manometer or gauge begins to oscillate, and the writing point *d* begins to trace a sinuous line *f*, the height of which above the line *e* indicates the variations which the blood pressure undergoes as well as its absolute amount. In

the diagram we observe that *f* presents large sweeping curves, each of which is marked by very numerous small curves; the former, as we shall afterwards state more particularly, represent the changes in the blood pressure which correspond with the respirations, the latter those which are dependent upon the state of the heart.

In fig. 7 are seen two exact copies of tracings obtained by means of the kymographion, the upper one indicating the variations in pressure in the carotid artery of a dog, the lower one that of a rabbit.

FIG. 8.



FICK'S MANOMETER.

A hollow spring filled with alcohol.

B stop-cock.

b free end of hollow spring connected with series of levers.

c lever bearing the writing point *e*, which is made to press against the revolving smoked cylinder.

D flexible tube connected with artery.

The height of the blood pressure at any given time during an experiment can be found by drawing ordinates from the curve traced at that time to the line of no pressure, and multiplying the result by two.

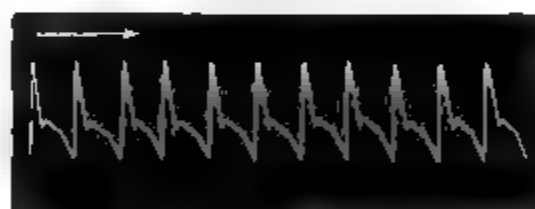
The oscillations of the mercury in the mercurial kymographion,

although of approximately the same duration as the pressure fluctuations which give rise to them, give no *exact* indication of the actual extent of these fluctuations; because the mercury, on account of its inertia, sets up oscillations of its own. In order to ascertain the course of the fluctuations in pressure, other manometers are used; for instance, a bent elastic tube filled with fluid which is expanded by pressure upon its contents (Bourdon's manometer, Fick's kymographion).

In the accompanying diagram (fig. 8) is shown one form of Fick's manometer. *a* is a hollow spring which is filled with alcohol. At *b* there is usually a tap. *d* is a flexible leaden tube. At *e* the free end of the hollow spring is communicated to a series of levers, and through them to the writing point *e*, which may be made to press gently against a blackened revolving disk. When the contents of the spring are subjected to increased pressure, the spring tends to open, the end *b* rises, and consequently *e* rises also.

Below is a tracing, taken with Fick's manometer, of the pressure in an artery.

FIG. 9.



TRACING OF THE CHANGES IN ARTERIAL PRESSURE CORRESPONDING TO EACH CARDIAC SYSTOLE, TAKEN WITH FICK'S MANOMETER.

The mean arterial pressure in the carotid artery of the dog varies between 130 and 190^{mm} (5.1–7.5 inches); in the rabbit it varies between 50 and 90^{mm}.

In the brachial artery of man the arterial pressure has been actually determined (Faivre) to be 110–120^{mm} (4.3–4.7 inches), but the results are almost certainly too low, having been obtained in cases of amputation in persons enfeebled by disease and loss of blood. In the human aorta the blood pressure has been estimated at 250^{mm} of Hg (9.8 inches), and we may assume that in the carotid artery of man it will be about 6 inches; these numbers can only, however, be looked upon as approximations to the truth.

In the pulmonary artery the arterial pressure is said to be about one-third as high as in the larger systemic arteries.]

The work done by the Heart. —The work done by the right ventricle (i.e. the product of the mass of blood raised into the height to which it is raised) is (three times) less, and its muscular coat therefore thinner, than that of the left. The work of one systole of the latter, reckoning the quantity of blood at 175 grms., and the aortic pressure at 250^{mm} Hg (= 3 mtr. of blood) may be reckoned at 0.525 of a kilogrammetre, and the work of twenty-four hours (seventy-five

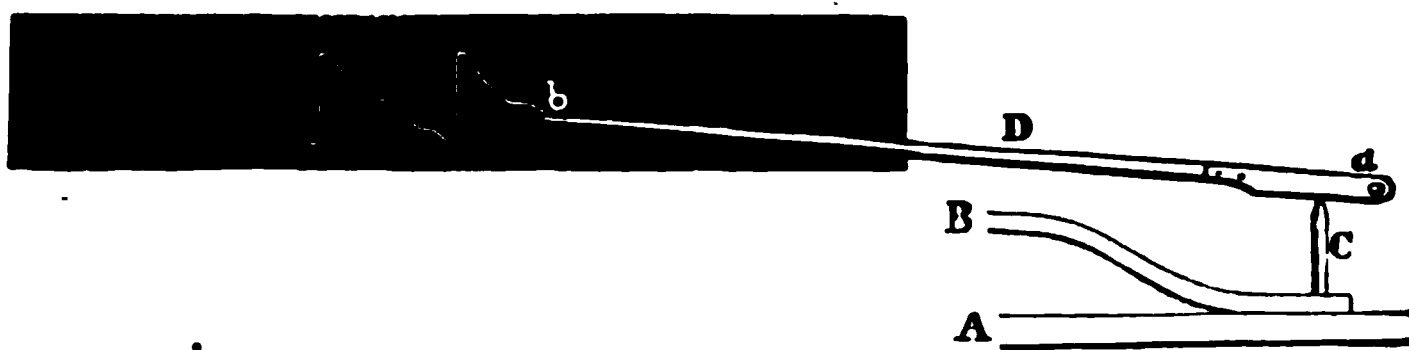
systoles in the minute) at 56,700 kilogrammetres. The work of the whole heart, therefore, amounts to about 75,600 kilogrammetres. Since, therefore, the weight of the heart is 292 grms., it would raise its own weight 10,788 mtrs. in one hour. As already shown, the whole of this work is converted into heat by friction in the vessels. Concerning the means which exist for preserving a constant pressure of blood, see below.

The Pulse.—The continuous stream of blood through the capillaries presupposes an almost constant tension of the arteries leading immediately into them, so that in these the increase of pressure corresponding to the systole can be scarcely appreciable. Following the arterial system, however, backwards to the heart, we find in every portion of it a regular fluctuation in pressure; that is, an increase of pressure corresponding to the systole, and a diminution answering to the diastole. This fluctuation of pressure, which can be easily demonstrated in any artery, is the more considerable the nearer it is to the heart, and therefore is greatest at the commencement of the aorta (and pulmonary artery), and least, almost unnoticeable, in the terminal arteries; this fluctuation of pressure is called the *pulse*. It does not occur synchronously throughout the whole arterial system, but each phase of it (for instance, its maximum) shows itself first nearest the heart; that is, the fluctuation in pressure travels—in the form of a *wave*—from the heart to the capillaries through the arteries, losing constantly in intensity. For the blood, pressed during systole into the commencement of the arterial system, at first increases the tension in that part alone; the next moment, however, this portion of the artery—distended beyond its diastolic volume—tends to relieve itself of its excess by its elasticity: the return of the blood is prevented by the closure of the semilunar valves; the surplus is therefore forced forwards, and, as in any elastic tube, the distension travels on towards the capillaries. If the arterial system ended in closed tubes, it is plain that the wave would run to the end in undiminished size, and be then reflected back again. But since the continual drain through the capillaries constantly diminishes the systolic excess in the arterial system, so that, according to Weber's theory, it entirely disappears before the following systole, the wave, during its course, becomes gradually smaller, until, at the end of its journey, it disappears. In certain cases, however, the pulse wave passes into the capillaries, and, through these, even into the veins; that is, in other words, in certain cases the plan described above is not carried out perfectly: the stream through the capillaries becomes no longer continuous, but the cardiac rhythm rules even in them:—this takes place when the resistance of an artery is diminished by its sudden enlargement, so that the balance hitherto existing between the resistance and the difference in tension of the arterial and venous systems becomes locally disturbed, as, for instance, by the division of the *vaso-motor* nerves (Bernard).

The speed of transmission of the pulse wave (not to be confounded with the speed of the blood current, to be afterwards considered) may be measured with a watch, by comparing the moment of passage of the wave in a distant artery with the moment of systole, or with the moment of the pulse in an artery near the heart. In round figures it may be said that the pulse wave travels at the rate of 9 metres or 29·5 feet per second (according to E. H. Weber its average rate being 28·5 feet). [The pulse wave is caused by an event—the systole of the left ventricle, which lasts about one-third of a second. As the wave travels, approximately at the rate of 9 metres per second, it is obvious that the commencement of the wave must have travelled to the furthest limits of the arterial system before the end of the wave has left the point where it originates; it may further be shown that the length of the crest of the pulse wave must be greater than that of the arterial system.]

In investigating the nature and phenomena of the pulse, both the changes in pressure of the blood contained within the living arteries, and the increase in size which occurs in every artery during the passage of the pulse wave, are the objects of observation. Naturally, it is only in the case of the lower animals that we can employ those instruments of research which teach us the exact changes which take place in the blood pressure under the influence of the pulse wave; of these instruments Fick's manometer and Marey's sphygmoscope furnish the most reliable information. The more precise study of the pulse in the human subject is carried out with the help of sphygmographs; the first of these instruments was devised by Vierordt, but it has been superseded by the sphygmograph of Marey. [The principle of Marey's sphygmograph may be learned by consulting the appended diagram, fig. 10.

FIG. 10.



SCHEMA OF THE SPHYGMOGRAPH.

A represents the artery which is indirectly pressed upon by the spring B, which through C transmits its movements to the lever a D; b is the writing-point tracing the pulse curve on a smoked piece of glass.

In this instrument we have a spring which is placed over the artery (usually the radial) so as to follow the vessel in its dilatation and contraction, and this spring communicates its movements to a sensitive lever furnished at its free extremity with a writing-

point which inscribes its movements on a tablet which can at will be made to pass at a uniform rate of speed in front of it.

If we examine a tracing taken with the sphygmograph of the movements of the radial artery (see fig. 10), we observe that the lever has traced a series of curves, each of which corresponds with

FIG. 11.



a single contraction of the left ventricle, with a single pulse wave. The line of ascent has been traced by the lever, during the distension, by the pulse wave, of the portion of artery over which the instrument has been placed; and its abruptness indicates that this act is one which takes place much more rapidly than that which is indicated by the more slowly falling line of descent traced by the lever. As we look at this line of descent we often observe that it is broken by two or more secondary rises, which lead us to conclude that on the great, or, as we may term it, *fundamental* pulse wave, there are superposed other minor waves.

The descending stroke in the pulse curve is traced by the lever as the artery, which had for a moment been disturbed by the great pulse wave, is returning more gradually to its normal condition. What is the nature of the wavelets which appear to indicate that once or twice, or sometimes even oftener, the emptying artery undergoes temporary increases of tension?

Of these secondary waves one is more constant than the others; it is distinctly seen in fig. 11. It is termed *the dicrotic wave*, and is present in all satisfactory pulse tracings; it is observed in an exceedingly exaggerated form in some cases of disease in which the pulse appears to the skilled touch of the educated physician to be double, the touch appreciating that two distinct distensions of the artery correspond to each ventricular systole. The latter morbid condition (*dicrotism*) has long been known to physicians, and is merely an exaggeration of the *normal dicrotism* which the study of sphygmographic tracings has revealed. The dicrotic rise has by many been supposed to be produced by a reflected wave of blood setting in from the peripheral arteries and flowing towards the heart. Were this view correct, the dicrotic rise should bear a different relation to the commencement of the great pulse wave in the different arteries; but it would appear that no such difference is to be observed, the dicrotic distension following the primary distension at an equal interval in all arteries, whether near to or far from the heart. We may, then, almost certainly conclude that the dicrotic rise is not due to a reflected wave.

Although the fact is not admitted by all, the bulk of the evidence appears to be in favour of the view that the dicrotic rise coincides in point of time very closely with the closure of the aortic valves. Admitting this, it would appear probable that the dicrotic wave is connected with, or generated by, the impact of blood against the closed semilunar valves and against the commencement of the aorta; the elastic rebound of the walls of which at this time probably reinforces the dicrotic wave.

There is another rise which is observed almost as frequently as the dicrotic rise in really good sphygmographic tracings, and which is situated higher up in the line of descent of the sphygmographic curve—which indicates a distension of the artery by a wave which actually precedes the dicrotic wave, and which may be termed the *predicrotic wave*. It appears probable that the predicrotic wave is an example of a wave of oscillation, *i.e.* 'of a wave due to the inertia of the elastic walls and of the contained fluid' exactly similar to the secondary waves which are observed to follow the primary wave when a moderate quantity of fluid is injected into an elastic tube containing water, such secondary waves being more marked the more sudden the stroke, the more extensible the tubing, and the less the pressure within it (Foster¹).]

The pressure of the blood in the capillaries cannot be measured; its changes, however, can be estimated from their size and from the amount of fluid which filters through them (Chapter II.) According to the scheme of the circulation previously described it must be constant, except when, as in the above-cited cases, the pulse wave is transmitted to the capillaries. Any diminution in the resistance of the vessels leading from the capillaries will increase it. It rises and falls, moreover, with the general pressure of the blood.

In the veins the blood pressure, appreciable with a manometer, is extremely low, being slightly negative in the large venous trunks, and increasing towards the periphery. Just as each rhythmic injection of blood into the arteries produces a rising wave in them, so each rhythmic removal of blood from the venous system would cause a falling wave passing from the capillaries, if this were not prevented by the auricles.

There are two other circumstances of such importance in the circulation of the blood, that they may be classed along with the contraction of the heart as causes of the circulation: they are the aspiration of the thorax, and the adventitious compression of the veins.

The Aspiration of the Thorax.—Owing to their position in a large cavity, which they (together with the lungs) must assist in

¹ Foster, *A Text-Book of Physiology*, p. 116.

filling, the heart and the large vascular trunks are dilated beyond their natural volume, and are consequently more completely filled with blood than they would be under other circumstances. This especially affects the more yielding portions—that is, the venous trunks and the auricles. As already mentioned when speaking of the heart, the aspiration of the thorax causes the blood flowing through the venous trunks opening into the heart to be immediately replaced by the flowing in of fresh blood from veins situated outside the thorax, and this essentially aids the circulation. Each inspiration, by its consequent enlargement of the cavity of the chest, further increases the negative pressure, and thereby causes over the whole mass of blood an aspiration in the direction of the thorax: but this aspiration will mainly affect the venous system. In the arteries it causes merely a slight decrease of tension; *on the other hand, it draws the venous blood powerfully towards the heart.* An ordinary expiration merely removes the inspiratory increase of the negative pressure; on the other hand, a *powerful* expiration, caused by muscular exertion, especially if an obstacle be opposed to the exit of the air by closure of the glottis (as in coughing), changes the negative pressure in the thorax into a positive one, compressing the heart and vessels (in particular the veins), and causes in the veins a serious stagnation, and in the arteries a less important increase in pressure. In consequence of this, the central end of a divided vein sucks in air during inspiration, and this may lead to fatal consequences by leading to embolism of the pulmonary capillaries: on the other hand, the veins swell considerably during a powerful expiration, particularly during coughing. If after a deep inspiration the glottis is closed, and a powerful attempt made at expiration, the positive pressure in the thorax becomes so great that the venous trunks are almost closed, less and less blood pours into the heart, and at last the circulation is entirely stopped (E. Weber). The action of these thoracic conditions on the arteries shows itself likewise in a regular fluctuation of the blood pressure (increase during expiration, decrease during inspiration), which is synchronous with the movements, not of the heart but of breathing, and is therefore four times as slow as the pulse.

[The respiratory waves which are seen in the kymographion curve are admirably shown in the appended figures, of which the upper is taken from the carotid artery of a dog and the lower from that of a rabbit.

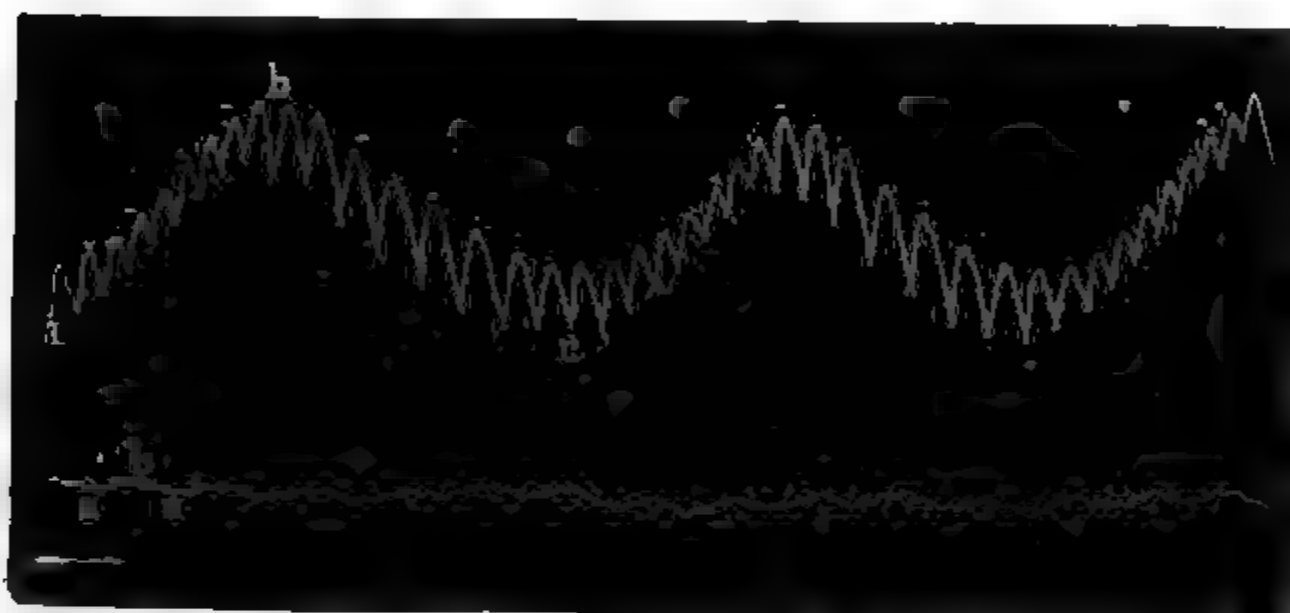
Examining the upper tracing, we observe that any one respiratory curve *a b c* is made up of a part *a b* which indicates a rising blood pressure, and of a part *b c* which indicates a falling blood pressure; moreover, that in the part *a b* the heart-beats succeed one another much more quickly than in the part *b c*.

Now, whilst these curves bear a certain relation to the respiratory movements, we have to observe that neither of the two

characteristic parts of the curve coincides with either inspiration or expiration.

The greater part of the curve from *a* to *b* takes place during inspiration, which is therefore accompanied by a rise in the blood pressure and by a more rapid contraction of the heart; the summit of the curve at *b* is, however, only reached after inspiration has ceased and expiration has commenced (Einbrodt,¹ Funke u. Latschenberger²). The pressure then gradually falls until the subsequent expiration causes it again to rise. The slowing of the heart, which takes place during the inspiratory fall of blood pressure, ceases to be observed after division of the vagi.

FIG. 12.



TRACINGS ILLUSTRATING THE FLUCTUATIONS IN THE ARTERIAL PRESSURE WHICH CORRESPOND TO THE RESPIRATORY ACTS.

These changes in the blood pressure and in the rate of heart-beat which accompany respiration, appear to depend in part upon the varying supply of blood to the heart during the various respiratory acts (more blood flowing into the heart during inspiration than expiration), in part, however, also upon the activity of the cardio-inhibitory centre and of the vaso-motor centre. In dogs which have been subjected to the action of curare and in which artificial respiration has been maintained and then stopped, fluctuations in the blood pressure somewhat similar to the normal respiratory curves are observed to occur (Traube's curves³).]

Transient, adventitious compression of the veins by the contraction of neighbouring muscles.—Any such compression of a portion of a vein must press its contents in a direction towards the heart, since the passage in the opposite direction is stopped by the self-closing venous valves. This compressing apparatus is in some places joined to an aspirating arrangement; thus the

¹ Einbrodt, *Wiener Sitzungsber.* 1859, p. 345.

² Funke u. Latschenberger, *Pflüger's Archiv*, Vol. xv. p. 426

³ Traube, *Gesammelte Beiträge*, Bd. 1.

portion of the femoral vein lying under Poupart's ligament sucks in the blood from the periphery at each turn in an outward direction of the upper part of the thigh, and empties it into the vena cava on each turn in an inward direction, or on flexion (Braune).

The movement of the blood in the veins consequently is as follows: when the blood has flowed through the capillary system, its speed, according to the above scheme, almost $=0$, because the tension in the arterial system is only sufficient to drive the necessary amount of blood (about 175 grms. in $\frac{1}{75}$ minute) through the capillaries. The force of the heart therefore, being entirely expended in overcoming this resistance (being converted into heat), has no influence on the flow of blood in the veins.¹ On the other hand the following forces come into action: 1. Gravity: this can only aid the circulation in the descending veins (as, *e.g.*, those of the head when upright), while on the other hand it checks it in ascending veins: the veins of the foot for instance, under the pressure of their high column of blood, would be so enormously dilated and stretched, and the resistance caused would be so great, that the whole movement of the blood in the lower extremities would be stopped. The other forces, therefore, which co-operate in the maintenance of the venous circulation are of the greatest importance, viz. 2. *The aspiration of the thorax*, particularly during inspiration, and 3. *The muscular movements of the body*. From what has been stated it follows that the venous circulation goes on very irregularly.

The movement of the blood in the *capillaries*, which may be observed under the microscope in transparent parts (for instance in the web and mesentery of the frog, in the omentum of the guinea-pig,—in the latter case on a hot stage, Stricker), frequently changes its direction in the branchings of their fine network. At the same time the movements of the blood corpuscles give one the opportunity of observing the unequal speed of the different layers of blood previously alluded to; those floating in the axis having the greatest, those next to the walls a far lower, rate of speed. In the finest capillaries, through which only one row of red blood corpuscles can force themselves at a time, the latter may frequently be seen to accommodate their shape to their surroundings—they become lengthened, bent, and curved, and pressed together until all shape is lost, and then again assume their natural form. For the emigration of the blood corpuscles, see the Appendix to this Chapter.

¹ This does not hold good in its entirety: the real conditions are more complicated than the theoretical (Weber's) statement given here, for in many cases the local tension of the artery exceeds this limit, and the blood enters the veins with perceptible velocity, frequently under such pressure that, if cut, the veins spurt. We therefore usually find included amongst the forces causing the venous flow 'the residue' of the motive power of the arterial system ('vis-a-tergo, vis inertiae,' &c.)

Velocity of the Circulation.

If a fluid be circulating through a system of tubes, the same quantity of fluid must flow through any collective cross section of the system during a given time. Whenever, on account of some obstacle, this condition is not fulfilled, if the system is dilatable, the section must become proportionately enlarged in front of the obstacle, and a repletion of vessels takes place. Thus, for example, the resistance of the capillaries causes the constant repletion of the arterial system. If, however, the circulation is in undisturbed progress, *the same quantity of blood must flow through any collective cross section of the vascular system during a unit of time.* It follows, moreover, from this, that *the speed of the current* in the various collective cross sections is *inversely proportional to the area of the cross section*: it is, therefore, greatest in the commencement of the aorta and the pulmonary artery, least (about 400 times less than in the aorta) in the capillaries. Similar conditions control the speed in the total cross sections of a single branched or unbranched vascular segment: thus, the blood flows at the same speed throughout the whole length of an unbranched vessel of uniform size.

But the quantity of blood which flows through any cross section of the vascular system during a unit of time, naturally depends on the number and strength of the contractions of the heart. Let n be the number of systoles during the unit of time, a the amount of blood contained in a ventricle; then the amount of blood m flowing in a unit of time through each section is represented by $m = na$, that is, in the human subject about 218 grms. per second.

The rate of flow through the individual vessels, which make up a collective section of the system, will, it is clear, depend principally on the resistance which they offer, for the speed will be the less the greater the resistance, *e.g.* in narrow vessels, which give off branches at large angles. That the speed, moreover, varies greatly in the different layers of a vessel, has been already shown.

Regular fluctuations of speed only take place when the plan of a continuous stream is not perfectly carried out, as is the case in arteries, through the influence of the pulse wave, and similarly in the capillaries and veins when the pulse wave, as will exceptionally occur, reaches them (p. 96). That the passage of the pulse wave must cause a momentary acceleration in each portion of the artery, follows from what has been before stated; for the wave crest increases tension at a particular place, while the tension is still of the diastolic height in neighbouring parts, and the speed increases with the difference in tension. In the capillaries and

veins, leaving out of the question the cases of exceptional presence of pulse, the speed would be constant were it not that, in the latter, there are many influences at work producing great irregularities.

The stream of blood through a vein may frequently be completely stopped; this may, however, be unproductive of harm, since most sets of capillaries have several efferent veins, so that if the stream of blood is obstructed or arrested in one, the blood flows more quickly through the others.

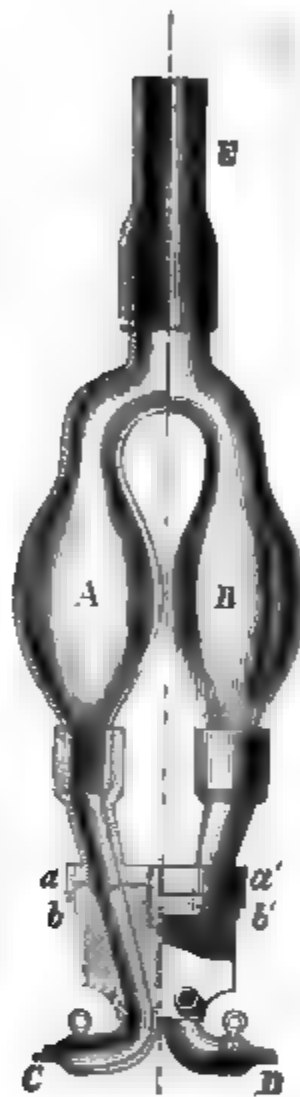
The following instruments have been employed to measure the speed of the current of blood in the arteries:—

1. Volkmann's hæmodromometer,¹ which consists essentially of a glass tube of known volume filled with water, which can suddenly be inserted into the stream of the artery. The time which the blood takes to run through the tube and displace all the water, is measured with a watch. On the same principle, but capable of giving much more reliable results, is the 'Stromuhr' of Ludwig.² [This instrument, which is shown in the accompanying woodcut (fig. 13), consists of two glass bulbs, A and B, of precisely equal capacity, and which communicate above by means of a curved glass tube which has a tubular opening upwards which admits of being closed by an india-rubber tube E and a clamp.

Below, the two bulbs A and B are cemented into bored metal sockets prolonged upwards from the cylindrical plate *aa'*; this plate is by a screw connected with a second bored piece of metal *bb'*, in such a manner that *aa'* may be rotated around *bb'*. When *aa'* is in the same relative position to *bb'*, as is shown in the drawing, then the interior of the globe A communicates with the open extremity of c, i.e. the tubular perforations of *aa'* are continuous with the tubular perforation in *bb'*. If, then, the plate *aa'* and its attached bulbs be rotated through an angle of 180° around *bb'*, the position of the globes in reference to the tubes is exactly reversed: then B will communicate with c, and A with d.

When an experiment has to be performed with the stromuhr, one of the bulbs is filled with olive oil, the other with defibrinated blood; c and A are inserted into the proximal and distal end of the artery in which the velocity of the blood-flow is to be determined. At first the position of *aa'* to *bb'* is such that the bulbs A and B are shut off from c and d. *aa'* is rotated so that the bulb containing oil (let us assume this to be A) is placed over the cannula inserted in the proximal end of the artery. Blood then flows in and drives the oil from A into B, whilst the defibrinated blood contained in the latter is injected into the distal end of the blood vessel. If the cubic capacity of the bulbs be known,

FIG. 13.



LUDWIG'S 'STROMUHR.'

A and B, blood bulbs.
a a', metallic plates connected with A and B, and rotating over *b b'*.

c and d, connectors, to be inserted into arteries

into the proximal and distal end of the artery in which the velocity of the blood-flow is to be determined. At first the position of *aa'* to *bb'* is such that the bulbs A and B are shut off from c and d. *aa'* is rotated so that the bulb containing oil (let us assume this to be A) is placed over the cannula inserted in the proximal end of the artery. Blood then flows in and drives the oil from A into B, whilst the defibrinated blood contained in the latter is injected into the distal end of the blood vessel. If the cubic capacity of the bulbs be known,

¹ Volkmann, *Hæmodynamik*, p. 185.

² Ludwig u. Dogiel, 'Die Ausmessung der strömenden Blutvolumina,' *Sitzungsber. d. k. böhm. Ges. d. Wissenschaft, Math.-phys. Cl.*, 1867, p. 200.

and the time taken by the oil to displace the blood contained in B be ascertained, we know the volume of blood which has, in the circumstances of the experiment, flowed through the artery in a given time. But this first observation can be checked by numerous repetitions. As soon as the oil has passed from A into B, the plate $a\ a'$ is rotated through 180° , and then B is in relation with the cardiac end of the artery; the oil contained in it will again be passed into A, the time measured, &c.]

2. The tachometer (employed by Vierordt¹) is a tube inserted in the artery; the tube contains a light pendulum. The movements, which may be observed externally, stand in a previously determined relation to the velocity of the stream, which acts on the pendulum. If the latter is joined to a sensitive lever, outside the tube, curves may be obtained whose ordinates will give the speed of the current ('dromograph,' Chauveau and Lortet²). 3. The determination of the amount of blood flowing from an open artery, the tension being maintained pretty constant by regulating the size of the artery (Vierordt).

Determinations by the above-mentioned methods have naturally not been made in the human subject. (In the carotid of dogs the speed varies from 200 to 700^{mm} per second.) In animals the speed in the capillaries is determined by direct microscopic measurement of the course a blood corpuscle runs over in a given time (E. H. Weber); in the human subject, by personal observation of the entoptic visible movements of the blood corpuscles in the vessels of the retina (Ludwig³); by the latter method Vierordt found them in himself = 0.6-0.9^{mm} in a second (compare Chap. X.). The speed in the veins may be measured with the 'Stromuhr' (Cyon and Steinmann⁴).

In order to measure the time in which a portion of blood travels through a given portion of the vascular system, or indeed through the whole round of the circulation, an easily recognisable salt (ferrocyanide of potassium) is injected into the central (cardiac) end of a vein, and the time noted at which it is detected (by chloride of iron), in samples of blood taken at short intervals from the peripheral end of the same vein (Hering⁵). The first discovered traces of the salt must have traversed the right side of the heart, the capillaries of the lungs, the left side of the heart, and the capillary territory corresponding to the vein which is experimented upon, before reaching the place where they are found. According to such experiments a complete circulation occupies 15.2 seconds in dogs, and about 23 seconds in the human subject.

Distribution of the Blood in the Body.

The quantity of blood contained in any portion of the body in a given time depends: 1. On the number and size of the afferent arteries. 2. On the speed of the current within them. The latter, as stated above, depends on many circumstances, particularly on their greater or less distance from the heart, on the number and angles of their branches, &c. For the changes in the size of an artery, see below under 'Innervation of Vessels,' where further particulars will also be found concerning the distribution of the blood in the body.

If one of the extremities be immersed in a vessel filled with

¹ Vierordt, *Die Gesetze der Stromgeschwindigkeiten*. Frankfurt, 1858.

² Chauveau, *Journal de la Physiologie*, 1860, p. 695; Lortet, *Recherches sur la vitesse du cours du Sang*. Paris, 1867.

³ Ludwig, *Lehrbuch der Physiol.* Vol. i. p. 354.

⁴ Cyon and Steinmann, *Bull. de l'Acad. des Sciences de St.-Petersbourg*. Vol. xvi. p. 266.

⁵ Hering, *Zeitschrift f. Physiologie von Tiedemann und Treviranus*. Vol. iii. p. 64.

water, which, with the aid of caoutchouc around the edge, can be accurately closed, and if the lesser end of the vessel be connected with a kymographion, any increase in pressure will indicate that more blood has flowed into the limb than has left it; if the rate of flow in the veins be constant, each increase in pressure indicates a greater, and each increase in pressure a less, rate of flow in the arteries (Fick¹).

The volume of a limb measured by the aid of such a contrivance ('Plethysmograph'), is subject to variations which are in part regular—depending upon the pulse, in part irregular; the latter are to be referred partly to contraction of the vessels of the limb, partly to general changes in the blood pressure, and partly to muscular contractions which expel venous blood (Mosso,² Frank,³ v. Basch⁴).

*Influence of the Nervous System on the Circulation of the Blood.*⁵

The nervous system has a direct influence on the movements of the blood, 1. by its control of the movements of the heart; 2. by its control of the calibre of the vessels, particularly of the smaller arteries, for the latter are supplied with muscles, on whose state of contraction their size depends. Not only is the supply of blood to individual organs regulated by changes in the capacity of a vessel, but change in the capacity of a large number of arteries, and the consequent change in the contents of the whole arterial vascular system, has a great influence on the activity of the heart.

1. Innervation of the Heart.

a. Intracardiac Centres.

The heart, removed from the body, or separated from all the nerves supplied to it, still beats for some time; in cold-blooded animals for days, in warm-blooded animals so long as a supply of oxygenized blood is provided. Its movements must, therefore, at least in part, be caused by a mechanism situated within itself, and the latter is supposed, with the greatest probability, to reside in the ganglionic cells (connected together by nerve fibres), which are

¹ Fick, *Untersuch. a. d. Züricher physiol. Laborat.* Vol. i. p. 1.

² Mosso, *Von einigen neuen Eigenschaften der Gefäßwand*: Ludwig's *Arbeiten*, 1874; *Movimenti dei vasi sanguigni nell' uomo*. Ac. Sc. di Torino, Nov. 1875.

³ Franck, *Du volume des Organes dans ses rapports avec la Circulation du Sang*. *Travaux du Laboratoire de M. Marcy*. Année 1876, p. 1. See also Marcy, *Mesure manométrique de la pression du sang dans les artères de l'homme*. *Travaux*, 1876, p. 309.

⁴ v. Basch, 'Die volumetrische Bestimmung des Blutdrucks am Menschen,' *Wiener med. Jahrb.*, 1876.

⁵ It is advantageous to refer to the influence of the nerves when considering the principal processes of molecular change, although by such anticipation many ideas are introduced, which are only explained in the Third Part of this work.

lodged in the muscular substance of the heart, particularly in the septum between the auricles, and at the junction of the auricles and ventricles (Remak¹). At least a portion of these ganglia must cause the *automatic* rhythmical contractions of the heart, and indeed the whole process of contraction (from the auricles to the ventricles) must be regulated and combined by them. In a heart which is at rest, but still excitable, one or more regular contractions of its various divisions may be produced, by reflex action, on applying different stimuli (mechanical, thermal, chemical, or electrical) to the substance of the heart: greater effect is obtained by stimulation of the inner than of the outer surface of the heart.

The causes of the constant rhythmical excitation of the intracardiac centres is altogether unknown. A supply of oxygen is a necessary condition (Ludwig, Volkmann, Goltz), as well as a temperature which must not be far removed from the normal blood heat of the animal.

Temperatures below 0°–4° and above 30°–40° C., stop the pulsations of the frog's heart (Schelske,² E. Oyon). The frequency of the beats increases with the temperature almost until the limiting point is reached. The strength of the contractions is greatest at low and medium temperatures, and is pretty constant; above 20°–30° the strength diminishes. The sudden action of high temperatures produces the phenomena of excitation of the vagus; if, however, the heart has been powerfully cooled before it is exposed to a high temperature, there occur rapidly succeeding contractions which ultimately give place to tetanus. When the heart has been stopped by heat, excitation of the sinus (which at other times stops the heart by exciting the vagus) causes tetanus of the ventricle (E. Oyon).

In general, even in warm-blooded animals, the frequency of the pulse increases with the temperature of the body.

In the frog's heart the principal ganglionic masses (Remak's ganglia) lie in the wall of the sinus venosus. After the separation of the latter, the heart ceases to contract, whilst the sinus itself continues to pulsate (Stannius³). Other injuries which merely affect the sinus cause the heart to stand still (v. Bezold). A second ganglion (Bidder's ganglion) lies near the junction of the auricles with the ventricle; if the heart which has been separated from the sinus venosus, and which is not pulsating, be divided in this region, that portion again commences to pulsate rhythmically in which the ganglion has been left; usually the ventricles, sometimes the auricles, or both auricles and ventricles. These pulsations are, however, temporary, and appear to depend upon mechanical irritation of Bidder's ganglion, which usually is not in a state of activity. (Even when this separation of auricles and ventricles is not effected, the heart which has been separated from the sinus, and which is motionless, may be made to pulsate for a time by a puncture into the line of junction of auricles and ventricles, H. Munk). Some attribute the arrest of the heart which follows its separation from the sinus venosus, to irritation caused by the section of the fibres of the vagus (Heidenhain). The hypothesis that inhibitory centres exist which have their seat in the auricles, and which are unable to control the combined motor powers of the sinus and the ventricle, whilst they can control the latter by itself (v. Bezold), is capable of accounting for the phenomena to which reference has been made, and is supported by some toxicological facts.

¹ Remak, *Müller's Archiv*, 1844, p. 463.

² Schelske, *Die Erregbarkeit der Nerven durch die Wärme*. 1860.

³ Stannius, *Zwei Reihen physiol. Versuche*. 1851.

Certain recent investigations have led to the surmise that even portions of the heart muscle which are free from ganglia may be capable of rhythmical pulsations when continued stimuli act upon them. If a cannula be tied into the ventricle of the frog's heart, below the auriculo-ventricular groove, the constricted apex (whose movements can be registered by means of a manometer connected with the cannula) usually stands still; if, however, oxygenated blood or certain saline solutions be introduced, pulsations occur (Ludwig and Merunowicz¹). All these results must, however, be interpreted with caution, inasmuch as these pulsations do not occur when in an otherwise uninjured frog the apex is first constricted and afterwards the ligature relaxed, so that the apex is fed with normal blood (Heidenhain, Goltz, Bernstein²). If the ligature be in the region of the auricles the pulsations occur in irregular groups (Ludwig and Lucani³). Even by constant currents, pieces of heart muscle free from ganglia appear to commence to pulsate.

The muscular substance of the ganglion free apex (connected with a manometer) evinces certain peculiarities; on exciting it with induction shocks of increasing strength it is found that the contractions which occur with the weakest efficient shock are of full strength, and do not increase though the stimulus be made stronger. According to some, even tetanus occurs when the excitations are very frequent (Ludwig and Bowditch,⁴ Kronecker⁵).

Nerve fibres connecting the ganglion cells with the muscular fibres of the heart have hitherto not been found. Excitation appears to be propagated from one muscle cell directly to the other, so that contraction travels along in both directions; the rapidity of transmission is about 10–30^{mm} per second (Engelmann⁶).

The behaviour of the cardiac ganglion to electrical stimuli is not sufficiently known. Single induction shocks lead to an accelerated systole when they act upon the heart during diastole (Marey). Tetanizing induction currents and powerful constant currents abolish the rhythm and lead to irregular movements which are accompanied by a powerful sinking of the blood pressure (Ludwig and Hoffa, Einbrodt, S. Mayer⁷). Constant currents of moderate strength throw the heart, which has been stopped in consequence of removal of the sinus, into rhythmical movements, in which occasionally the contraction of the ventricle precedes that of the auricles (v. Bezold,⁸ Bernstein, Foster and Dew-Smith⁹); this phenomenon requires further investigation.

It is doubtful whether the blood pressure has an influence upon the pulsations of the heart. The statement that, after the cardiac nerves have been divided, an increase of the blood pressure (brought about, for instance, by compression of the aorta, contraction of small arteries induced by excitation of the vaso-motor centre or of important vaso-motor nerves such as the splanchnics) leads to an increased frequency in the contractions of the heart, has lately been

¹ Merunowicz, 'Ueber die Chemischen Bedingungen für die Entstehung des Herzschlages,' *Bericht. d. sächs. Akad. zu Leipzig*. 1875, pp. 252–298.

² Bernstein, 'Ueber den Sitz der automatischen Erregung im Froschherzen,' *Centralblatt f. d. med. Wissenschaft*. 1876, p. 433.

³ Luciani, *Eine periodische Function des isolirten Froschherzens*. Ludwig's *Arbeiten*. 1872.

⁴ Bowditch, *Ueber die Eigenschaften der Reizbarkeit, welche die Muskelfasern des Herzens zeigen*. Ludwig's *Arbeiten*. 1872, p. 139.

⁵ Kronecker, *Das charakteristische Merkmal der Herzmuskel-Bewegung*. Ludwig's *Festgabe*. 1875, p. 173.

⁶ Engelmann, 'Ueber die Leitung der Erregung im Herzmuskel.' *Pflüger's Archiv*. Vol. xi. p. 465.

⁷ Ludwig u. Hoffa, *Zeitschrift f. rat. Medicin*. 1850. Vol. ix. p. 107.

⁸ V. Bezold, 'Physiologie d. Herzbewegung.' *Virchow's Archiv*. Vol. xiv.

⁹ Foster and Dew-Smith, 'The Effects of the Constant Current on the Heart,' *Journal of Anat. and Physiol.*, vol. x.; and *Studies from the Physiol. Lab. in the Univ. of Cambridge*. Part III. p. 1.

contradicted by Knoll¹ and Nawrocki,² and confirmed by Tschiriew.³ In the case of the frog's heart it is asserted that increase in the blood pressure slows the contractions (Marey).

b. Inhibitory Nerves.

Even the nerves which enter the heart from the cardiac plexuses, and which are derived partly from the pneumogastric, partly from the sympathetic, exert an influence upon the movements of the heart. The fibres contained in the vagus possess the power, when they are continuously irritated by mechanical, chemical, or electric means, of *slowing* (or weakening, Ludwig and Coates⁴) the contractions of the heart; and when subjected to a more powerful irritation, of bringing the whole heart to a standstill in diastole (Ed. Weber,⁵ Ludwig,⁶ Budge⁷). In mammalia, and especially in man, such an excitation, originating in the origin of the vagus in the medulla oblongata, is kept up throughout the whole of life, so that section of the vagi suddenly increases the frequency of the pulse.

The vagus contains, in addition to inhibitory fibres, others which accelerate the heart; after poisoning with atropia, which paralyses the inhibitory fibres, excitation of the vagus quickens the heart, Schmiedeberg.⁸ Very slight excitations of the vagus, even without atropia, occasionally cause an increase in the number of heart-beats (Schiff,⁹ Giannuzzi).

In relation to the heart, the vagus belongs to the group of '*regulating nerves*' (consult on this subject Chapters IX. and XI.)

In man the vagus can be occasionally irritated by mechanical means, as by pressure (Czermak, Concato).

When both vagi are subjected to the same degree of irritation, it is found that the right vagus possesses, in the lower animals, a more powerful inhibitory action on the heart than the left (Masoin,¹⁰ Arloin, and Tripier¹¹). A short interval elapses between the time of commencement of the irritation of the vagus and that of the display of its inhibitory action ('Latent Period,' Donders, Prael, and Nuel¹²). The irritation of the vagus need not necessarily be the same as that required to induce tetanus generally, in order to induce the inhibitory influence, but it suffices if it consists of separate irritations following one another rhythmically with moderate rapidity (v. Bezold). During the arrest of the heart brought about by irritation of the vagus, any immediate excitation of the organ gives rise to a single and regular contraction. When a vagus has, by repeated stimulation, been exhausted, the beatings of the heart recommence. If, when one vagus has been exhausted, the other be stimulated, it too is in-

¹ Knoll, *Sitzungsberichte d. Wiener Akademie vom Juli 18, 1872.*

² Nawrocki, *Ueber den Einfluss des Blutdruckes auf die Häufigkeit der Herzschläge*, Ludwig's *Festgabe*, p. 205.

³ Tschiriew, 'Ueber den Einfluss der Blutdruckschwankungen auf den Herzrhythmus,' *Archiv f. Anat. u. Physiol.* 1877. Physiol. Abtheil, p. 116.

⁴ Coates, *Wie ändern sich durch die Erregung des N. Vagus die Arbeit und die innern Reize des Herzens?* Ludwig's *Arbeiten.* 1870.

⁵ Weber in Wagner's *Handwörterbuch der Phys.* Vol. iii. p. 31.

⁶ Ludwig und Hoffa, *Henle's Zeitschrift f. rat. Med.* Vol. ix. p. 107.

⁷ Budge, *Archiv. f. phys. Heilk.* Vol. v. p. 319.

⁸ Schmiedeberg, *Ludwig's Arbeiten.* 1871, p. 46.

⁹ Schiff, *Physiologie*, 1859, pp. 187 and 417.

¹⁰ Masoin, *Bull. de l'Acad. Roy. de Méd. de Belgique.* 3rd series, vol. vi. p. 4.

¹¹ Arloin et Tripier, *Archives de Phys. norm. et path.*, July 1872.

¹² Donders, *Proceedings of R. Acad. of Sciences of Amsterdam*, 1869-70, No. 2.

capable of affecting the heart (Tarchanoff and Puelma¹). This is undoubtedly not always the case (Gamblee and Priestley).

In the heart of the frog, the phenomena due to irritation of the vagi may be induced by exciting the *sinus venosus*, to which the fibres of the vagus run. Poisoning with curare or atropia, as well as powerful cooling, paralyses the terminations of the vagus in the heart; nicotia stimulates them first, and then paralyses them.

Muscaria causes the heart to stop in diastole, and its effect is not counteracted by curare or nicotia, but by atropia (Schmiedeberg²). These facts would appear to indicate that muscaria stimulates an inhibitory apparatus; not the vagus endings which curare or nicotia act upon, but probably an *inhibitory centre*, which the peripheral ends of the vagus communicate with, and the influence of the stimulation of which this centre transmits to the heart. This inhibitory apparatus would appear to be paralysed by atropia but not by nicotia.

The Inhibitory Centre is in warm-blooded animals continually in action; and, like the respiratory centre which is quite close to it, is perpetually under the influence of numerous afferent nerves, whose excitation causes the heart to beat more slowly so long as one or both vagi are uninjured. To this group belong most different sensory nerves (Lovén,³ Kratschmer), the vagus itself (v. Bezold, Donders, Aubert and Rœver⁴; one vagus receiving a central excitation whilst the other is intact), the cervical and abdominal sympathetic cords and the splanchnic (Bernstein⁵); mechanical excitation (striking) of the abdominal viscera likewise, in a reflex manner, slows the pulse (Goltz,⁶ and it does so most readily in inflammatory conditions, Tarchanoff). On the other hand, the activity of the inhibitory centre is lessened by inflating the lungs (Hering).

The activity of the inhibitory centre, like that of the respiratory centre, is increased by the state of the blood which leads to dyspnoea (compare Chap. IV.), and may, indeed, assume a similarly rhythmical character (observed when air containing carbonic acid is introduced into the lungs, Traube); a rhythmically increased activity of the inhibitory centre actually coincides, even in the normal condition, with each inspiration (Donders). Increased arterial pressure in the brain increases the excitation (activity) of the inhibitory centre.

After division of the above-mentioned afferent nerves, it is said that the tonic activity of the vagus centre ceases; which would prove that the excitation of the vagus by its centre is a reflex phenomenon (Bernstein). The reflex actions referred to in the preceding paragraph may be prevented by powerful stimulation of sensory nerves.

¹ Tarchanoff et Puelma, *Archives de phys. norm. et Path.* 1875, p. 498.

² Schmiedeberg, *Untersuchungen über einige Giftwirkungen am Froschherzen*, Ludwig's *Arbeiten*. 1871, p. 41 et seq.

³ Lovén, 'Ueber Erweiterung von Arterien durch Nervenirregung,' *Ber. d. k. sächs. Ges. d. Wissenschaft.* 1866, p. 85

⁴ Aubert u. Rœver, *Pflüger's Archiv*. Vol. i. p. 224.

⁵ Bernstein, 'Zur Innervation des Herzens,' *Centralblatt f. d. med. Wissenschaft.* 1867, No. 1.

⁶ Goltz, *Vagus und Herz*, Virchow's *Archiv*. Vol. xxvi. pp. 1-33.

c. Accelerating Nerves.

Stimulation of the medulla oblongata, or of spinal cord in the cervical region, causes an increased frequency of pulse by exciting the *accelerating nerves* which proceed to the cardiac plexus through the *rami communicantes* of the lower cervical nerves, and through the *ganglion stellatum*; direct excitation of these nerves in any part of their course leads to the same result (v. Bezold,¹ M. and E. Cyon,² Schmiedeberg, &c.) The centre which presides over these accelerating nerves, the conditions of the activity of which are altogether unknown, appears to reside in the medulla oblongata; it is not constantly in a state of activity, for section of the spinal cord is attended by no slowing of the pulse, providing that the indirect slowing due to changes in the blood pressure have been prevented by previously dividing the splanchnics (brothers Cyon).

Seeing that the cervical spinal cord contains vaso-motor fibres whose excitation raises the blood pressure and thereby, according to some, increases the frequency of the pulse, the existence of accelerating nerves of the heart could only be proved by exciting these nerves directly. Proof of a more indirect kind is, however, afforded by the fact that excitation of the spinal cord, even after the most important vaso-motor nerves (the splanchnics) have been divided, leads to an acceleration of the pulse; and conversely, that after the cervical nerves have been cut across, stimulation of the spinal cord leads to a lesser degree of acceleration (only an indirect acceleration, or, according to some, to no acceleration) than before.

The occurrence of the accelerating action on direct stimulation follows it much more slowly than do the effects observed on stimulating the vagus; not only does the effect follow much more slowly (i.e. the latent period is very much longer), but it disappears more slowly. If excitation of the vagus is superposed upon excitation of the accelerating nerves, it leads to the same degree of relative slowing as when the nerves are inactive; the action of the one nerve does not interfere with that of the other. They have, therefore, in all probability different relations to the heart, and are not purely antagonistic (Ludwig, with Schmiedeberg, Bowditch,⁴ and Baxt⁵).

2. Innervation of Blood Vessels.

The calibre of the arteries varies, quite independently of their elasticity, with the degree of contraction of the smooth muscular fibres which are contained in their coats. The latter are influenced by a variety of circumstances; thus, contraction of arteries is

¹ V. Bezold, *Untersuchungen über die Innervation des Herzens*.

² M. and E. Cyon, 'Ueber die Innervation des Herzens von Rückenmarke aus,' *Archiv für Anatomie und Physiologie*. 1867.

³ Schmiedeberg, *Ueber die Innervationsverhältnisse des Hundeherzens*, Ludwig's *Arbeiten*. 1872. p. 34.

⁴ Bowditch, *Ueber die Interferenz der retardirenden und beschleunigenden Herznerven*, Ludwig's *Arbeiten*. 1872.

⁵ Baxt, *Ueber die Stellung des N. Vagus zum N. accelerans Cordis*, Ludwig's *Arbeiten*. 1876.

increased by cold, and diminished by heat. Even the blood pressure and the quantity of gases which the circulating blood contains appear to exert an influence on the contraction of arteries (Ludwig and Sadler,¹ Hafiz,² and Mosso³); chiefly, however, the calibre of the arteries depends upon the state of irritation of the nerves which govern the muscular structures of the vessels, the *vaso-motor nerves* (Bernard⁴). In the case of the majority of these a continuous '*tonic*' state of excitation has been proved to exist, so that their section leads to a paralysis of the muscular fibres of vessels, to a dilatation of the artery, to an increased flow of blood through the organ concerned, and, consequently, to its becoming red, to its temperature becoming higher, and to an increased transudation through its capillaries. The flow of blood may, under these circumstances, increase so much, that the blood may pass into the veins without having lost its arterial colour, and the pulse waves may be propagated even to the veins (Bernard. Compare p. 104.) The irritation of the peripheral end of vaso-motor nerves must, conversely, lead to a narrowing of arteries, and to a diminution of the flow of blood, even to its complete stoppage, so that the parts of the body concerned necessarily become pale, cold, and the seat of scantier transudation from the blood (parenchymatous juices, secretions, &c.)

Nothing is yet known concerning the relations, if any, of vaso-motor nerves to veins. It has often been submitted that capillaries are endowed with contractility, but nothing definite in relation to this matter has been made out.

A *peristaltic contraction* of the arteries, passing from the main trunks towards the capillaries, would drive the blood actively into the capillaries, and thus aid in the circulation. That this takes place during life is not positive. After destruction of the motor power of the heart, however, an active emptying of the arteries into the veins is brought about by stimulation of the vaso-motor centres (Goltz, Thiry, v. Bezold), and it is probable that the emptiness of the arteries after death is to be attributed to the persistent activity of the same centre. Blushing and erection of the penis are the best known phenomena produced by the action of nerves on the local movements of the blood.

The vaso-motor nerves run partly in spinal, partly in sympathetic trunks; for instance, in the cervical portion of the sympathetic for the scalp, conjunctiva, and salivary glands (Bernard⁵) (in part also in the N. Auricularis magnus, Schiff and Lovén); in the anterior roots of the spinal nerves for the lower extremities (Pflüger⁶), first, however, joining the rami communicantes of the

¹ Sadler, *Ueber den Blutstrom im den ruhenden, verkürzten und ermüdeten Muskeln des lebenden Thieres*, Ludwig's *Arbeiten*. 1870.

² Hafiz, *Ludwig's Arbeiten*. 1870.

³ Mosso, 'Von einigen neuen Eigenschaften der Gefäßwand,' *Bericht. d. k. sächs. Gesellsch. d. Wissenschaft*. 1875, p. 305.

⁴ Bernard, *Le grand Sympathique*. 1854.

⁵ Bernard, 'Recherches expérimentales sur les nerfs Vasculaires,' *Comptes Rendus*. 1862.

⁶ Pflüger, *Med. Centralztg*. 1855 u. 1856 (quoted by Wundt).

sympathetic (Bernard). The vaso-motor nerves of the upper extremities proceed from the middle dorsal roots to the sympathetic chain, thence to the first thoracic ganglion, and thence through the rami communications to the plexus brachialis (E. Cyon¹). The capacious vascular system of the viscera² receives its fibres from the splanchnics, which are, consequently, the most influential of the vaso-motor nerves (v. Bezold, Cyon, and Ludwig). The lungs receive their vaso-motor nerves, whose *tonus* is but small, not as was formerly erroneously surmised, from the vagus, but from the cervical portion of the spinal cord, through the first thoracic ganglion (Brown Séquard, Fick and Badoud, Lichtheim).

A common *central organ* for the vaso-motor nerves is situated in the medulla oblongata, by stimulating which, the spinal cord and sympathetic being uninjured, contraction of all the small arteries is produced, and, as a consequence, increase of the blood pressure in the arterial trunks, and turgescence of the heart (Ludwig and Thiry³); for a description of this see Chapter XI. This central organ is constantly in action, and this explains the tone of the vaso-motor nerves. Division of the spinal cord in its cervical portion abolishes this tone, thus causing dilatation of all the arteries.

As, however, after some time the tone is (in part) restored, and disappears again when the spinal cord is destroyed, we must conclude that the spinal cord also contains vaso-motor centres, which, however, are not usually in a state of tonic activity (Goltz, Vulpian).

Even some time after division of the vaso-motor nerves the arterial tonus returns (Schiff). This points to the existence of more widely diffused *ganglionic* centres, in immediate relation with the blood vessels; centres the existence of which is supported—by the phenomena of inflammation described at page 119—by the independent pulsations of blood vessels which are observed in many localities, even after division of the vaso-motor nerves,—by the action which heat possesses of causing vascular dilatation, and, lastly, by the existence of nerves whose excitation causes the dilatation of blood vessels.

Vascular dilatation as an effect of the excitation of nerves had long been observed to occur in certain regions (Bernard,⁴ Schiff, Lovén,⁵ and others); lately the general existence of vaso-dilator

¹ E. Cyon, *Ueber die Wurzeln durch welche das Rückenmark die Gefässnerven für die Vorderpfote aussendet. Ludwig's Arbeiten.* 1869, p. 62.

² This vascular division is so large, that it can contain almost the whole of the blood of the body: on tying the portal vein, for instance, animals subjected to the operation die of anæmia, because the whole of the blood remains in the visceral vessels (Ludwig and Thiry).

³ Ludwig und Thiry, 'Ueber den Einfluss des Halsmarkes auf den Blutstrom,' *Sitzungsber. d. Akad. d. Wissenschaft zu Wien.* 1864, p. 421.

⁴ Bernard, *Journal de la Physiologie.* 1862, p. 416.

⁵ Lovén, 'Ueber die Erweiterung von Arterien in Folge einer Nervenirregung,' *Ludwig's Arbeiten.* 1866, p. 1.

nerves has been ascertained (Goltz,¹ Heidenhain, and Ostroumoff,² Kendal and Luchsinger³). The most probable hypothesis in reference to these nerves is, that they are inhibitory nerves for the ganglia of the blood vessels, whose function it is to transmit to the latter the action of vaso-motor nerves, or which under certain circumstances can originate an independent tonus. The vaso-dilator nerves are not in a state of continual activity, i.e. they possess no tone; their central organs appear to be disturbed in a similar manner to those of the vaso-motor nerves.

In many parts of the body the vaso-dilator nerves run in separate paths from the vaso-motor; in other parts they are found mixed with the vaso-motor nerves. In the first case their discovery is easily effected by the method of stimulation. Thus stimulation of the corda tympani leads to dilatation of the blood vessels of the submaxillary glands (Bernard,⁴ compare Chap. II.), and of the anterior part of the tongue (Vulpian⁵). Similarly acts stimulation of the glosso-pharyngeal nerve upon the posterior part of the tongue (Vulpian); stimulation of the nervi erigentes causes erection, i.e. dilatation of the arteries and corpora cavernosa of the penis (Eckhard,⁶ Lovén). In the head one can observe, even after section of the vaso-motor nerves (cervical-sympathetic), that the ear blushes under the influence of psychical stimuli (Schiff).

The muscular arteries dilate on stimulation of their nerves or of the spinal cord, and independently, too, of the commencement of muscular contraction (Ludwig with Sczelkow, Hafiz, Sadler, and Gaskell⁷). In the extremities the nerve trunks contain both kinds of vascular nerves (Goltz⁸); on weak, especially on rhythmical stimulation of the trunks, the effect of the vaso-dilator nerves preponderates, and the same usually follows on exciting the divided trunks some days after their section, as the vaso-motor fibres are the first to degenerate; on the other hand, powerful stimulation of fresh nerves leads to vascular constriction. The sciatic nerve derives both constricting and dilating fibres from the sympathetic (Ostroumoff, Kendal, and Luchsinger).

The activity of the vaso-motor centre depends upon conditions which are very similar to those which affect the inhibitory centre for the heart. Centripetal nerve fibres which intensify the tonic excitation of the centre (so-called '*pressor*' fibres) are contained in the vagus, specially in its superior laryngeal branch, and even more abundantly in the cervical sympathetic (Aubert and Roever⁹); further, every excitation of a sensory nerve leads to a general contraction of blood vessels (Lovén). Certain centripetal (*depressor*) fibres contained in the vagus, which in some animals are contained in a separate branch which arises from the heart, the *ramus depressor* (Cyon and Ludwig¹⁰), diminish the vascular tone.

¹ Goltz, *Pflüger's Archiv*. Vol. ix. p. 174; vol. xi. p. 52.

² Heidenhain, *Pflüger's Archiv*. Vol. v. p. 40. Ostroumoff, *Pflüger's Archiv*. Vol. xii. p. 219.

³ Kendal und Luchsinger, *Pflüger's Archiv*. Vol. xiii. p. 197.

⁴ Bernard, *Leçons sur les liquides de l'Organisme*. Vol. ii. p. 272.

⁵ Vulpian, *Leçons sur les Vaso-Moteurs*. 1874.

⁶ Eckhard, *Beiträge*. 1868.

⁷ Sczelkow, *Sitzungsberichte d. Wien. Akad.* vol. xlv. Hafiz, *Ber. d. k. sächs. Gesellschaft der Wissenschaften zu Leipzig*, vol. xxii. (1870), p. 215. Sadler, *Ber. d. k. sächs. Ges. zu Leipzig*, vol. xxi. (1869), p. 189. Gaskell, *Ludwig's Arbeiten*, 1876; *Journal of Anat. and Physiology*, vol. xi. pp. 360 and 720.

⁸ Goltz, *loc. cit.*

⁹ Aubert und Roever, *Centralblatt*. 1868.

¹⁰ Cyon and Ludwig, *Ber. d. k. sächs. Gesell. zu Leipzig*. 1866, p. 807.

The centripetal irritation of many sensory nerves causes dilatation of the vessels distributed to the part supplied by the nerve (Lovén). According to another account all sensory nerves contain, like the vagus, both pressor and depressor fibres (Latschenberger and Deahna¹).

The *tone* of the vaso-motor centre is, further, dependent upon the gases contained in the blood. When the quantity of carbonic acid increases (in asphyxia, when an atmosphere containing much carbonic acid is inhaled) the smaller arteries generally contract with an increase of the intracardiac pressure and a distension of the heart (Thiry); this contraction intermits, however, in a regular rhythmical manner (Traube), and the rhythm coincides with the respiratory excitations (Hering). These phenomena occur even when the carotids have been occluded, whereby the blood which is stagnant in the brain becomes fitted to induce dyspnoea (Nawalichin, S. Mayer; compare Chap. IV.)

The inhalation of irritating vapours through the nostrils exerts a *pressor-influence* through the medium of the trigeminus (5th) nerve. Similarly acts mechanical irritation of the stomach, and especially of its serous coat. The pressor action of sensory nerves is only present as long as the brain is intact (E. Cyon). The respiratory variations in the blood pressure which were previously alluded to, appear in part to be in relation with the rhythmical activity of the vaso-motor centre (Schiff).

Many of the facts which have been adduced point to the existence of a complex regulating system, by which the velocity and the pressure of the blood flowing into the capillaries are maintained constant or within the limits necessary to the functional activity of the organs. It is specially to be noticed that a high pressure in the arterial system, and in the heart, on the one hand, increases the activity of the heart, on the other (through the *N. depressor*), diminishes the resistance which it has to overcome, by causing a relaxation of the peripheral arteries. Our knowledge is as yet far too incomplete to permit of our understanding the complete mechanism. (For the regulation of the blood pressure in the brain consult Chap. XI.)

[*Summary of the Relations of the Nervous System to the Organs of the Circulation.*]

It may probably facilitate the comprehension of this somewhat intricate subject by the student who is just entering upon its study, if a somewhat dogmatic summary be given of the conclusions to be drawn from a study of the preceding pages.

From what has preceded, the reader has learned that the central organ of the circulation, the heart, possesses an intrinsic nervous mechanism of its own, in virtue of which it continues to pulsate in

¹ Latschenberger u. Deahna, *Pflüger's Archiv*. Vol. xiii. p. 212.

an orderly, rhythmical manner when separated from all other nervous connections. What the precise relations of the nervous mechanism to the muscular substance may be is not yet known.

This intrinsic nervous mechanism is connected with the cerebro-spinal axis by (*A*) efferent fibres, (*B*) afferent fibres.

A. The efferent fibres, which proceed from the cerebro-spinal axis to the intrinsic nervous mechanism, are of two kinds. The first and most important are contained in the pneumogastric nerve, and proceed from a nerve centre situated in the medulla oblongata, termed *the inhibitory centre*, which is in a state of perpetual activity. These fibres of the vagus are, like the centre whence they proceed, perpetually in action (though the intensity of the activity varies), and the result of their activity is to inhibit (i.e. to moderate or restrain) the contractions of the heart, which beats normally more slowly than it would do were they in abeyance; we know of no anatomical facts teaching us how these inhibitory fibres of the vagus are connected with the cardiac motor ganglia. Physiological facts offer, however, strong presumptive evidence in favour of somewhat complex apparatuses intermediate between the terminations of the vagus and the motor ganglia.

The second set of efferent fibres also appear to proceed from a centre in the medulla oblongata, but pass down the spinal cord, issuing from it at the lower part of the cervical region, and, passing through the last cervical or first dorsal sympathetic ganglia, make their way in sympathetic trunks to the cardiac plexuses, and so to the intrinsic nervous mechanism. These nerves are not usually in a state of activity, and the result of their intermittent activity is to accelerate the movements of the heart. The complexity of their connection with the intrinsic mechanism is evidenced by the long period which elapses between their stimulation and the result of that stimulation.

B. The intrinsic nervous mechanism transmits to the cerebro-spinal axis *afferent* nerve fibres, which are contained in the trunk of the pneumogastric, or in some of its cardiac branches. These fibres may be divided, according to their functions, into three groups. Firstly, some appear to be fibres ministering to common sensibility; secondly, some are excito-cardio-inhibitory, i.e. are in relation to the inhibitory centre in the medulla, the activity of which they can increase, so as to lead in a reflex manner to a slowing of the heart; thirdly, others are depressors of the tone of the vaso-motor centre. These fibres thus establish a relationship between the nervous apparatus of the heart and that of the blood vessels.

The muscular elements of all the arteries of the body receive efferent nerve-fibres, termed *vaso-motor* fibres, but which, to distinguish them from other fibres to be presently mentioned, we may designate *vaso-constrictor fibres*, which proceed from so-

called vaso-motor centres, of which the chief is situated in the medulla oblongata. These fibres are in a state of perpetual activity, though the intensity of that activity, like that of the respiratory and inhibitory centres, undergoes slight rhythmical variations; the result of the activity of the vaso-motor nerves is to maintain the arteries in a state of semi-contraction called *arterial tonus*, or *tone*, which varies in intensity according to the greater or less activity of the vaso-motor centre or centres.

But in addition to the vaso-motor nerve fibres there are other efferent fibres connected with blood vessels, the result of the activity of which is opposed to that of the vaso-motor fibres; these may be termed the *vaso-dilator* nerves; unlike the vaso-constrictor fibres, they are usually not in action. When we attempt to realize the arrangements of these dilator nerves we are at first met by great difficulties. We know of no nerve fibres in the body which, when excited, lead to the elongation of muscular fibres. The excitation of one nerve may, it is true, undo the mechanical effect of stimulation of another nerve, by bringing into action a second set of muscular fibres which will counterbalance the effect produced by the contraction of the first set, but there is no evidence of the existence of different arrangements of muscular fibres in arteries. How, then, may the action of vaso-dilator nerves be explained? By supposing them to be inhibitory nerves which, when excited, are capable of preventing the transmission of the activity originating in vaso-motor centres.

As is mentioned in the text, numerous physiological facts prove that, in certain regions, local nerve centres are connected with vascular areas; anatomical proofs that such connections are almost universal are continually accumulating. Those ganglia in close proximity to arteries have doubtless the most intimate relations both with vaso-constrictor nerves and vaso-dilator nerves. When the latter are inactive, the state of activity, originating in a more central vaso-motor centre, may be supposed to travel unmodified through the local centre presiding over the vascular area. Given, however, a sufficiently powerful excitation of vaso-dilator nerves, and an effect will be produced, in the local ganglion, which will enormously increase the resistance to the transmission of vaso-motor impulses, and the result will be that the vaso-motor nerves of the part will cease to be active, and the arteries will dilate.

The student will therefore, in constructing an ideal schema of the innervation of blood vessels, introduce as necessary elements, first, a centrally situated vaso-motor centre, or rather centres, whence proceed vaso-constrictor nerves, which, passing through a second peripherally disposed ganglionic centre or centres, are ultimately distributed to the muscular elements of blood vessels; the first-named centre being in connection with some fibres which increase its activity, and by others which diminish it. Secondly, a

centrally situated vaso-dilator centre, or centres, whence proceed vaso-dilator nerves, which ultimately end—not in contractile elements—but in the above-mentioned peripherally disposed ganglia, through which the vaso-motor nerves directly or indirectly pass.]

Frequency of the Pulse.

From the facts which have been adduced, it follows that the frequency of the pulse, the height of the blood-pressure, and the velocity of the circulation depend upon very numerous influences. The mean frequency of the pulse in the adult amounts to seventy-two beats in the minute; in the foetus, however, it is much greater (184); the pulse falls to the twenty-first year. In old age the frequency again appears to increase.

The frequency of the pulse is very liable to vary; thus strong mental emotions exert a powerful action upon it, probably through the vagi. The following are the influences which chiefly affect the pulse rate. *Temperature*: heat increases, cold diminishes the frequency of the pulse (either by a direct action, or more probably in a reflex manner). *Movement* increases the frequency. *Position of the body*: when the body is vertical, though the muscles be at rest, the frequency of the pulse is greater than when it is horizontal; the cause of this is unknown. *Respiration*: during inspiration the pulse is slower than during expiration: further, the frequency of the pulse is greater during digestion than during the intervals between meals, and it is finally greater in persons of the female sex and of small stature than in those of the male sex and of large stature.

Numerous medicinal substances and poisons exert an action on the frequency of the pulse, as soon as they enter the blood. They do so partly by a direct action on the cardiac ganglia, partly by exciting or paralysing the *vagus-centre*, or the fibres of the *vagus*, especially its terminations in the heart, and they possibly even act on the *accelerating* system. The above-mentioned influences on the pulse may also be due to an action exerted on the vaso-motor apparatus.

[Action of Medicinal Agents upon the Circulation.]

As the action of various poisons on the heart has thrown considerable light upon the mechanism of its innervation, the following classification of the chief heart poisons, according to their probable mode of action, is appended.

1. *Nicotia*, *Curare*, *Conia* paralyse the communications of the *vagus* with the inhibitory ganglia (in some cases producing a preliminary stage of excitation). Stimulation of the *vagus* is unable to slow or stop the heart; this effect, however, follows stimulation of the *sinus venosus*.

2. *Muscarin* and *Jaborandi*¹ stimulate the inhibitory apparatus, and so cause the heart to stop in diastole; their action is undone by the subsequent application of atropia, which is therefore an antidote to them; they are not, however, capable of antagonizing atropia.

3. *Calabar Bean* and its alkaloid *Physostigmia* increase at first enormously the excitability of the vagus and stimulates the inhibitory mechanism. Though not acting so intensely on any part of the mechanism as the poisons in Class II., and therefore not actually stopping the heart in diastole, it probably affects parts of the mechanism which they leave intact, as is evidenced by two facts: 1. That it removes the paralysis of the inhibitory mechanism induced by atropia; whilst, 2. Atropia removes the stimulating effects which it has induced.

4. *Atropia*, *Hyoscyamia*, and *Daturia* paralyses the whole inhibitory mechanism. Excitation of the vagus and of the *sinus venosus* are without effect. Muscarin has no effect; its effects on the heart are completely antagonized by Calabar bean.

5. *Aconitia*, *Veratria*, *Digitalin*, *Delphinia*, *Antiar*, act chiefly as muscular poisons, arresting the ventricular portion of the heart in powerful systole, and affecting the elasticity of the cardiac walls.]

APPENDIX.

EXIT OF BLOOD CORPUSCLES FROM UNINJURED VESSELS.

Emigration. Diapedesis.

UNDER abnormal conditions both red and colourless blood corpuscles may leave vessels without rupture of their walls ('Diapedesis'). The escape of the red corpuscles occurs during stoppage of the venous current. In consequence of the high pressure thus resulting, first the plasma is pressed out, and then the blood corpuscles; these, after being squeezed until all shape is lost, are pressed out like a fluid mass; afterwards they resume their original form (Cohnheim²). The same thing also occurs under other influences which are not mechanical; for instance, by the action of salts on exposed vessels (Prussak, denied by Cohnheim). Colourless corpuscles leave the vessels during inflammation either alone or

¹ Langley, 'The Action of Jaborandi on the Heart,' *Journal of Anatomy and Phys.*, 1876; *Studies from the Physiological Laboratory in the University of Cambridge*, Part II. 1876, pp. 53-67.

² Cohnheim, 'Ueber Entzündung und Eiterung,' *Virchow's Archiv*, vol. xl. 1867. 'Ueber venöse Stauung,' and vol. xli. 220.

together with a few red ones. After an enlargement of the small arteries and veins has been caused in a manner which is not yet understood by inflammatory action, and the speed of the current within them has been considerably lessened, a separation takes place of the colourless elements, which move slowly along close to the vascular walls, and at last become stationary, whilst the red ones flow on in the axis of the vessels. In the veins and capillaries the colourless corpuscles are then seen to pass through the vascular walls, displaying amœboid movements, and to appear outside as 'pus corpuscles' (Cohnheim). The formation of the above marginal layer may be explained either by the unequal speed of the various layers of blood, which would cause the spherical colourless corpuscles to roll gradually to the periphery, especially when the blood stream has become sufficiently slow (Donders, Cohnheim), or by a peculiar adhesiveness of the colourless corpuscles, which causes them, when the current is sufficiently slow, and they have accidentally fallen against the vascular wall, to adhere to it (Hering). Whether the passage of the corpuscles outwards happens in consequence of active amœboid movements (Cohnheim) or by a kind of filtration (Hering, Samuel), further, whether the passage takes place through openings (stomata), which exist preformed in the wall of the vessel, into the lymph-canal system, is as yet unknown.

CHAPTER II.

SOURCES OF LOSS TO THE BLOOD.

Secretion.

THE term 'secretion' in its widest sense denotes all those processes in which substances quit the blood in an altered or unaltered condition. The products of such processes are called 'secretions,' and may be regarded as of two sorts, viz. :—

1. Those liquids or gases ¹ derived from the blood, which exude from the internal or external surfaces of the body. Those yielded by internal surfaces (in cavities or canals)—called 'secretions' in the restricted sense—are destined for particular uses (*e.g.* in digestion), and are for the most part again taken up by the blood after undergoing a certain amount of change. Those yielded by external surfaces—called 'excretions'—are, on the contrary, lost to the body, although certain of them (*e.g.* the sebaceous and sudoriparous excretions) have certain functions in connection with the surfaces where they appear.

It will be seen that in their origin there is no difference between secretions and excretions; certainly the fact of their being liberated at internal and external surfaces respectively does not create a fundamental distinction. If we must keep them separate it will be best to regard those substances as excretions which are incapable of further use in the organism and whose retention by it would be harmful. To this class belong certain ultimate results of oxidation—carbonic acid, urea, &c.; and the respiratory and urinary products would, therefore, be the chief excretions. Frequently all the substances given off by the body, irrespective of their origin, are called excretions. If this definition be adopted, we must add to those just mentioned the following, the essential constituents of which are not at all, or only indirectly, derived from the blood :—1. The fæces, *i.e.* the indigestible parts of food mixed with those constituents of the alimentary secretions which are not reabsorbed by the blood vessels. 2. Epithelial exuviations (*i.e.* the cast-off portions of epidermis, hair and nails). 3. Ova and semen.

2. Those liquids derived from the blood which bathe the tissues of the body,—parenchymatous juices, muscle juice, the fluid moistening connective-tissues, &c.

Inasmuch as the solid portions of the tissues (cells, fibres, &c.) derive the material of which they are composed from the various parenchymatous juices,

¹ Gaseous secretions are treated of in Chapter IV.

and therefore immediately from the blood, every constituent of the body may be looked upon as a secretion. This process is, however, so imperfectly understood that we cannot pause to discuss it now. For the same reason we can here only refer, in general, to the secretion of the parenchymatous juices.

I. SECRETION IN GENERAL.

Physical Processes.

All fluids separated from the blood must pass through the walls of closed capillary vessels. It would seem that the only instance, during health, of a fluid passing through ruptured vessels is the menstrual flux: and even this may turn out to be a case of diapedesis. (See p. 119.)

The physical forces which bring about the passage of fluids through membranes are filtration and diffusion.

By filtration we understand the passage of a liquid under the influence of pressure through the pores (not the physical, intermolecular spaces, but the coarser, mechanical interstices) of a body such as a membrane. Just as in the ordinary process of filtering the weight of the substance to be filtered forces the liquid through the filter, so the tension of the blood vessels forces out some or all of the fluid constituents of the blood; for the pressure of the fluids surrounding the capillaries (parenchymatous juices) is generally less than the pressure of the blood in the vessels.

The amount of the filtered fluid increases with the difference between these two pressures. This difference is made more marked, 1, by relieving the tension in the neighbourhood of the capillaries, as in the withdrawal of the parenchymatous fluids or the reduction of the atmospheric pressure by cupping, &c.; 2, by increasing the tension of the capillary walls, which may be brought about (as was mentioned previously): *a*, by increasing the blood-pressure all over the body: *b*, by widening the arteries conducting blood to the part, *e.g.* by relaxing the normal contraction of their circular muscles by the application of heat, or by cutting off the influence of vaso-motor nerves. The converse operations, viz. diminution of blood-pressure, application of cold, and abnormal irritation of vaso-motor nerves will diminish the amount of the filtered fluid. This partly explains the influence of the nervous system upon secretion (see below). Filtration is affected also by the nature of the filtering fluid. True solutions pass through the medium unchanged. Viscid fluids, such as solutions of albumin, starch, and gum, filter less perfectly, a portion only of their contained substances, in amount varying with the pressure, being able to percolate. If indeed the pressure is very slight, the whole is retained on the filter. Under slight pressure, therefore, the blood loses by filtration water, salts, sugar, &c., which form true solutions; while under a greater pressure it is deprived of more or less of its albumin, fibrinogen, &c.

Diffusion (or osmose) is the intermixing of fluids through a membrane, independently of any difference of pressure on the two sides, often even in opposition to hydrostatic pressure. For this purpose it is not necessary that the membrane should be porous, the essential molecular interspaces of a homogeneous membrane being all that are required. (The most homogeneous membranes known are the so-called 'precipitation-membranes' which are formed at the surface of contact when one of two solutions capable of producing a precipitate is allowed cautiously to flow over the other, M. Traube.) In diffusion two liquids are required, while in filtration it is only necessary to have a liquid on one side of the membrane, the other being presented to the air or to

a vacuous space. Diffusion, moreover, can only take place between liquids of different kinds, while filtration may occur between those of the same kind, provided that each is subjected to a different pressure. The essential condition of diffusion is that the membrane should be saturated simultaneously by both liquids; the object of the process is the complete chemical equalisation of the fluids on the opposite sides of the membrane. According to the latest researches the passage of a substance through a membrane (endosmose) takes place, if there is on the other side of the membrane a liquid capable of dissolving the substance and having an affinity for it; and if the molecules of the body are somewhat less than the molecular interstices of the membrane. Endosmose takes place more quickly, the greater this affinity ('Endosmotic force') the smaller the molecules of the substance, and the larger the interstices (M. Traube). Endosmotic force is very great in the case of strongly hygroscopic substances. Certain complex bodies of great molecular weight (p. 49 *et seq.*) are incapable of diffusing through most membranes on account of the large size of their molecules. Such substances are albumin, hæmoglobin, gum, &c., which have been denominated 'colloids' by Graham, on account of their non-existence in a crystallized form, in contradistinction to 'crystalloids,' or substances which admit of crystallization. Solutions of colloids are somewhat viscous, not altogether fluid, and when concentrated by evaporation they do not suddenly assume the solid condition by the separation of crystals, but they gradually, and as a whole, assume that condition. Other writers (Vierordt, Jolly) consider the essential element in the process of diffusion to be the interchange between a portion of the diffusing substance, and an amount of the solvent liquid on the other side of the membrane: and the quantity of the solvent liquid which passes through for every unit of weight of the substance they call its 'endosmotic equivalent.'

As the blood is everywhere surrounded by fluids of a different chemical composition, and under a lower pressure than itself, it is plain that in nearly all cases of secretion both filtration and diffusion must play a part.

The purely physical processes of filtration and diffusion can only yield fluids containing the constituents of liquor sanguinis in various proportions. It has not been ascertained with certainty whether such simple separations occur. The nearest approach to them are the so-called transudation fluids, viz. the fluids found normally in the various cavities of the body (*e.g.* in the pericardial, peritoneal, and pleural sacs, in the cerebral ventricles, &c.); and the pathological fluids of dropsical cavities and œdematous tissues. Their principal constituents are water, salts, sugar, urea, varying amounts of albumin, fibrinogen, and sometimes also fibrinoplastin. The presence of fibrinogen may be demonstrated by the setting-in of coagulation on the addition of fibrinoplastin and the fibrin-ferment (*e.g.* in the form of a well-squeezed blood-clot). If the transudation-fluid contains at the same time fibrinoplastin, coagulation occurs spontaneously on withdrawal from the body; but, as a rule, only slowly, on account of the fibrinoplastin being present in such small quantities.

It has lately appeared very probable that the fluids found in the various cavities above mentioned should, in part at least, be regarded as lymph (Chapter III.); for not only have lymph corpuscles been seen floating in them, but direct communications have been traced between the cavities containing them and the lymphatic vessels (von Recklinghausen).

Chemical Processes.

Most secretions contain, in addition to the substances which are common to them and the blood, certain specific constituents, for the production of which the above-mentioned physical processes cannot alone account. It is necessary, therefore, to assume that certain chemical changes take place in the transuded fluids, the seat of which, or at least the impulse to which, must most probably be sought for in the cells with which the various secretions come into contact. Such cells are, in the case of parenchymatous juices, the cells or corpuscles of the tissues in which they arise; in the case of free secretions, the gland-cells.

The only difference, therefore, between parenchymatous and free secretions appears to be that the former remain enclosed in a fine cellular network, while the latter pass through a thin layer of cells (in the glands) and so quit their place of origin.

As the specific constituents of the various secretions belong, for the most part, to a class of bodies whose nature and origin are unknown, nothing can with certainty be said about the nature of the chemical processes supposed to take place in the cells of the various tissues and glands. Certain of these specific substances are, however, undoubtedly the result of the oxidation of some of the constituents of blood: and, as secretion is accompanied by a manifestation of energy, viz., as Ludwig has directly proved in the case of the salivary glands, by an evolution of heat, it is probable that all the chemical processes of secretion are merely processes of oxidation. This is further supported by the facts that, during the production of a secretion rich in its characteristic elements, more of the oxygen conveyed through the arteries to the gland is used up, as is indicated by the darker colour of the venous blood; and that secretion becomes impossible as soon as the supply of arterial blood is prevented, notwithstanding that the other necessary conditions are fulfilled. (Consult the section on Saliva.)

The formation of specific constituents appears in the case of many glands to be a process consisting of two stages. The first stage of the process consists in the continual synthetical formation of a mother substance—'zymogen;' the second in a decomposition of this zymogen, which takes place at the time of secretion, and which results in the liberation of the active ferment. This process, which had already, from analogy with the process going on in muscle, been assumed to occur (Hermann), has lately been proved in the case of the pancreas (Heidenhain).¹

¹ Heidenhain, *Beiträge zur Kenntniss des Pankreas*. *Pflüger's Archiv.*, Bd. X. (1875).

[It is only fair to mention that Mr. A. Liversedge published in 1874 (*Journal of Anat. and Phys.*, p. 28) the results of a research 'On the Amylolytic Ferment of the Pancreas' (from the Physiological Laboratory in the University of Cambridge), which led him to the conclusion that after the ready-formed ferment has been removed from a pancreas a regeneration of the ferment takes place, and which led him to surmise the existence of an 'antecedent of the ferment.']

In certain secretions the specific constituents are derived from the disintegration of cells. This is known to be the case with milk and the mucous, salivary, and sebaceous secretions; and it is probably also the case with others.

Organs of Secretion.

Free secretions are generated in special organs. The simplest form of secreting organ is a membrane provided with blood-capillaries on the one side and a layer of epithelium cells on the other; it has, moreover, nerves, the terminations of which are probably in direct connection with secreting cells. Such a form of glandular apparatus is that which serves for the secretion of the fluids filling the serous and synovial sacs, bursæ and sheaths. Most secretions, however, require a larger surface than a simple smooth membrane can afford. To supply this the membrane presents a single or branched, tubular or sacculate involution of its surface, upon which the secretion is poured out (mucous membrane, skin). Every layer of the originally smooth membrane follows the course of the sacculations; an examination of any part, therefore, would show, externally, a supporting stroma of connective tissue containing blood vessels, and often also muscular fibres; and internally an epithelium, the cells of which often become modified in form at the bottom of an involution, passing there into special secreting cells. Such an involuted secreting surface is called a *gland*. All transudations through the sides of the blood vessels must, therefore, pass through the layer of cells before occupying the hollow of the gland as a secretion, or reaching the surface, the sacculations of which forms the gland. There is another way in which the secreting surface may be increased, viz., by processes (villi), or projections such as are seen in synovial membranes.

If the involutions of the glandular surface are branched, the gland is said to be 'compound'; if they, or their branches, are like tubes or cylinders, the gland is called 'tubular' (sweat glands and gastric follicles, kidneys, testicles, &c.); if like sacs, 'racemose' (mucous, sebaceous, and salivary glands, &c.) In the case of compound glands, the tubular structure which leads into the gland, and into which the gland-products are emptied, is called the 'excretory duct.' This is frequently provided with an enlargement which serves as a reservoir (urinary bladder, vesiculæ seminales); or it may be connected with such a reservoir by means of another duct (gall-bladder). The so-called 'ductless' glands (spleen, lymphatic glands, follicles, suprarenal capsules, thymus, thyroid) are really not glands; they will be discussed in Chapters IV. and VI.

Influence of Nerves on Secretion.

In every act of secretion there is probably a nervous influence at work. This has been distinctly proved in many cases. It may assume the form of a first impulse to the act; or it may be evi-

denced by a quantitative or a qualitative alteration of the products, brought about by nervous excitation.

As in several glands (*e.g.* in the salivary glands, Bernard) the influence on secretion is connected with that on the blood-circulation through the gland, we might be inclined to explain the former as dependent upon the latter. The nervous system may influence secretion by its action on the circulation, which, leading to dilatation or narrowing of the arteries, may bring about, 1, changes of pressure in the gland capillaries, and, therefore, filtration-changes; 2, changes in the chemical processes dependent on the greater or less quantity of oxygen brought to the gland. Inasmuch as nervous influence may bring about a secretion which is in abeyance (in glands cut out of the body, Ludwig), even when the circulation is suspended, and as secretion may proceed when filtration is impossible, we must conclude that the influence of the nervous system upon secretion cannot be explained by its mere action upon the circulation. (By preventing the escape of a secretion the pressure in the excretory duct of a gland may, under nerve-stimulation, be raised above that in the arterial branches supplying the gland, and yet secretion proceed, Ludwig.¹) Recently anatomical changes have been discovered to occur in the glandular substance under the influence of nerve irritation (Heidenhain; see *Saliva*). It must be assumed, therefore, that, beside the vaso-motor, there are other specific 'secretory' nerve fibres, which have a direct, but as yet unintelligible, influence on the processes of secretion.

The influence of the vaso-motor nerves, apart from that of the proper secretory fibres, is conclusively proved (Bernard) by the coincidence of secretion and circulation-changes, which has already been pointed out. From the nature of the case their influence is principally upon the process of transudation; and they, therefore, affect the quantity and state of concentration of the secretion. The influence of the nervous system upon the chemical processes of glands, due to its power of modifying the supply of oxygenated blood to them, is uncertain, although we know that a supply of such blood is necessary for continuous secretion. (A gland cut out from the body, when its nerves are stimulated, yields its secretion only at first, even though by the production of artificial oedema a rich supply of fluid has been stored up within.)

An attempt has in recent times been made to prove anatomically the existence of secretory nerves. The statement upon which this attempt is founded, that a direct communication exists between nerve-fibres and secreting cells (Pflüger²), has, however, been often contradicted.

¹ *Zeitschrift f. rat. Med. N. F.* Bd. 1, p. 255; *Lehrbuch*, vol. ii. p. 214.

² Pflüger, *Die Endigungen d. Absond. Nerv. in d. Speicheldr.* Bonn 1866. See also C. Kupffer, *Die Speicheldrüsen von Periplaneta Blattia orientalis und ihr Nervenapparat.* Ludwig's *Festgabe*, 1875, p. lxiv.

II. INDIVIDUAL SECRETIONS.

A. Parenchymatous Tissues and their Secretions.

The methods hitherto used of obtaining the fluid secreted by parenchymatous tissues have failed to yield it pure enough, or in sufficient quantities, for the purposes of examination. They consist either in expressing the juices from tissues which have been deprived, as far as possible, of their blood, or in extracting the constituents of those juices one by one by means of various solvents (ether, alcohol, water, acids). Our knowledge of the composition and formation of the parenchymatous secretions is, therefore, extremely scanty. It is often even doubtful whether the substances thus obtained from a tissue should be referred to its fluid or its structural elements. We can only suppose in reference to their origin that their peculiar constituents (gelatin, fat, colouring matters, &c.) are formed from the fluids which transude from the blood vessels by the influence of the cells of the tissues, and probably under the control of special (trophic) nerves (Chapter IX.) It is further assumed that the transuded fluids are yielded in excess, which excess is returned to the blood by the lymphatics which absorb it (Chapter III.) The specific substances which are formed are in part insoluble, and become the structural elements of the tissues. Hence it follows that a purely chemical consideration of the fluid and formed constituents of parenchymatous tissue is not yet possible, and that the whole history of the development of the tissues can only be treated of from a morphological point of view. It will only be necessary, therefore, in this place, to state briefly, without any attempt at classification, the facts which have been ascertained respecting the chemical composition of the various parenchymatous tissues.

1. *Osseous Tissue*.—Pure osseous tissue (after the removal of the periosteum, marrow, &c.) contains a great excess of inorganic salts. Perfectly dried bones (bones contain about 2 per cent. of water) exhibit a very constant composition, which is different for different kinds of animals. In man there are 68 parts per cent. of salts, and 32 per cent. of organic matter (Zalesky). The salts are 84 per cent. of tribasic calcium phosphate ($\text{Ca}_32(\text{PO}_4)$), 1 per cent. of tribasic magnesium phosphate ($\text{Mg}_32(\text{PO}_4)$), 7.6 per cent. of other salts of calcium (CaCO_3 , CaCl_2 , CaFl_2), and 7.4 per cent. of alkaline salts (NaCl , &c.)

The organic portion consists almost entirely of a *gelatigenous* substance, which yields gelatin on boiling, especially after the addition of acids.

The osseous tissue of compact and spongy bones presents the same composition. This constancy of composition has led to the assumption that the organic portion is not merely mechanically impregnated by the mineral, but that the two are chemically combined (Milne-Edwards, jun., Zalesky).

Dilute acids deprive bone of its salts, and leave behind the animal portion, which is soft and resembles cartilage. Subjection to heat, on the contrary, destroys the animal matter, leaving a white, porous, inorganic mass (calcined bone). In both cases the bone retains its original external shape.

Connected with bone are the other calcareous tissues, e.g. teeth. Enamel, which contains very little water, possesses only 4 per cent. of organic matter, and is analogous to bone in its composition.

Nothing is known about the formation and regeneration of bone-tissue, except the morphological appearances presented in the various stages.

2. *Cartilaginous Tissue*.—Besides water and the constituents of the corpuscles, cartilage contains chiefly *chondrogenous* substance, elastin, and small quantities of inorganic salts.

Nearest to cartilage stands the tissue of the cornea, which on boiling yields a body resembling chondrin: it contains, in addition, much fibrino-plastic substance.

3. *Connective Tissue*.—In connective tissue the following elements have been recognised (Kühne):—(1.) The substance of the fibrillæ, a gelatigenous substance. (2.) An interfibrillar cementing substance, which can be extracted by lime-water or baryta-water (Rollett), the extract containing mucin. (3.) Elastin. (4.) Corpuscles, composed mainly of albuminous elements, and frequently containing fat. In foetal and some other tissues the gelatigenous substance is replaced by a mucin-yielding substance.

4. *Muscular Tissue*.—See Chapter VIII.

5. *Nervous Tissue*.—See Chapter IX.

B. Fluids of Cavities.

These fluids are not secreted by glands, but by the epitheliated membrane ('serous membranes,' &c.) lining the cavities where they are formed. From their composition they are regarded as simple transudations, the essential constituents of which have already been enumerated (p. 121). Their quantitative relations are extremely various, and cannot be referred to here. The following fluids may be regarded as simple transudations:—the cerebro-spinal fluid, the aqueous humour, and perhaps also the amniotic and allantoic fluids. The pericardial, pleural, and peritoneal fluids were formerly placed in the same category; but since they communicate directly through apertures with the lymphatic vessels (von Recklinghausen,¹

¹ V. Recklinghausen, *Die Lymphgefäße*, 1862.

Oedmansson,¹ Ludwig and Dybkowsky²), they must be considered as lymph (Chapter III.)

The following fluids of cavities have special constituents:

1. Synovia contains, in addition to the products of transudation, mucin (0·2 to 0·6 per cent.) and fat (0·06 to 0·08 per cent.) Numerous exuviated epithelial cells are also present.
2. The fluids of bursæ mucosæ and synovial sheaths contain a gelatinous material which has not yet been investigated.

The way in which the secretions of this class are used up and replaced is not understood.

C. Glandular Secretions.

1. ALIMENTARY SECRETIONS.

1. *Mucus*.

The mucus of the alimentary canal is secreted by glands which are lined by an epithelium resembling that of the region in which they are situated. In the mouth, pharynx, and œsophagus, the glands are small and racemose, and contain scaly epithelium; in the stomach (especially in the neighbourhood of the pylorus) and in the intestine they are simple, or slightly compound and tubular, and the epithelium is cylindrical. Mucus is a clear, slimy, ropy, alkaline fluid, consisting essentially of a solution of mucin, and also sometimes of albumin, in which the normal salts of the blood, especially NaCl, are dissolved. The mucus of the intestine contains, in addition, certain ferments which confer upon it special properties, and is, therefore, considered separately under the name of intestinal juice (see below). As a rule, mucus contains morphological elements in the form of (1) small, round, nucleated cells, resembling the colourless blood-corpuscles—the so-called mucous corpuscles—which are considered to be the young cells of the mucous glands; (2) fragmentary or entire cells of scaly epithelium from the mucous membrane, frequently adhering together by their edges as in their natural condition. The slimy nature of mucus fits it admirably for the purpose of lessening the friction between the walls of the alimentary canal and their contents.

Pure mucus may be obtained from the mouths of animals after ligaturing the ducts of all the salivary glands. It may be inferred from the morphological elements of mucus that mucin arises only through the disintegration of gland-cells (compare the salivary, sebaceous, and milky secretions). The influence which nerves exert upon the secretion is yet unknown.

¹ Oedmansson, *Virchow's Archiv.*, vol. xxviii. p. 361.

² Ludwig and Dybkowsky, *Arbeiten aus der Phys. Anstalt in Leipzig*, 1866.

As mucin does not appear to be capable of reabsorption, it most likely all passes out of the body in the fæces, while some of the remaining constituents of mucus probably find their way back into the blood.

2. Saliva.

The three different kinds of saliva from the parotid, submaxillary, and sublingual glands are very watery, colourless alkaline secretions of low specific gravity (1·004–1·009). Besides the usual products of transudation (among which are found very small quantities of albuminous bodies, albumin and globulin), they contain, as specific constituents, (*a*) mucin, of which the sublingual saliva possesses the most, the submaxillary less, and the parotid least; (*b*) a hydrolytic ferment, *ptyalin*, which converts starch into dextrin and sugar, this conversion taking place rapidly if the starch is in the form of a paste, and still more rapidly if it is subjected to the temperature of the body; (*c*) sulphocyanides (potassium-sulphocyanide). Moreover, saliva, and especially, as it would seem, sublingual saliva (Donders), contains morphological elements—salivary bodies—resembling closely mucous corpuscles; these ‘salivary cells’ enclose granules which exhibit active molecular movements. Mixed saliva contains also mucus and exuviated squamous epithelial cells from the cavity of the mouth.

In order to obtain the various kinds of saliva separately, use is made, in man, of pathological salivary fistulæ; except in the case of the parotid gland, where the saliva may be collected through a fine tube introduced into Steno’s duct, which opens in the side of the cheek opposite the second or third upper molar tooth. In the lower animals artificial fistulæ may be established. Ptyalin may be thrown down mechanically by causing a precipitation of calcium phosphate in saliva; it may then be extracted from the precipitate by water, and re-precipitated from the watery solution by alcohol. It is not an albuminous body (Cohnheim¹). The power of converting starch into sugar belongs to each of the three kinds of human saliva; but it is best shown in mixed saliva formed in the cavity of the mouth by the admixture of saliva from all the glands with mucus. In the lower animals, however, the three kinds do not all possess this power; for, in general, the three kinds of saliva are secreted in individual animals in proportions regulated by the food they usually take. The conversion into sugar takes place very rapidly, and is not prevented by the presence of a moderate amount of acid—a circumstance which is of importance in digestion. A given quantity of saliva cannot convert an indefinite quantity of starch into sugar (Paschutin). Potassium sulpho-cyanide, CN.KS, the presence of which may be demonstrated by the blood-red colouration which occurs on the addition of ferric-chloride, is not a constant constituent of saliva, and is found most frequently in mixed saliva from the mouth, especially if the teeth are decaying.

As an example of the quantitative composition of saliva, the following analysis of human mixed saliva may serve (Bidder and Schmidt). In 1,000 parts—water 995·16, solid constituents 4·84, containing epithelium 1·62, soluble organic matters 1·34, inorganic matters 1·82, almost one half of the last being alkaline chlorides.

¹ Cohnheim, *Virchow's Archiv*, vol. xxxviii. p. 241.

Secretion.

The secretion of saliva is, as may be demonstrated, under the control of the nervous system, the influence of which has been more fully investigated in this case than in that of any other secretion in the body. Without the operation of this influence secretion is completely inactive (C. G. Mitscherlich, Ludwig¹). During life, the excitation of secretory nerves would seem to take place always in one of two ways: either, in a reflex manner, on irritation (1) of the sensory and gustatory nerves of the mouth, (2) of the vagus, probably of those fibres proceeding from the digestive apparatus (Oehl,² though this is doubted by von Wittich,³ Nawrocki⁴); or on (voluntary) stimulation of the nerves to the masticatory muscles. Saliva is therefore secreted (*a*) on irritation of the cavity of the mouth by sapid substances or mechanical, chemical, thermal, or electrical stimuli, (*b*) in certain conditions of the stomach (nausea), and (*c*) during the movements of mastication. The centripetal fibres, which, on irritation, lead reflexly to secretion, run in the course of the fifth, the glosso-pharyngeal, and the vagus. The secretory fibres run in the course of the facial, the fifth, and the sympathetic.

Irritation of sensory nerves far removed from the glands, *e.g.* of the central end of the ischiatic nerve may also cause, by reflection, the secretion of saliva (Owsjannikow and Tschiriew).⁵

Among the secretory nerves we must distinguish two species (Bernard⁶, Eckhard⁷, von Wittich³) which, on irritation, produce differences, not only in the character of the secretion, but also in the vaso-motor phenomena: nevertheless, as was previously pointed out, we are not entitled to explain the former as dependent upon the latter. Irritation of fibres of the first kind induces narrowing of the arteries supplying the gland, the blood reaching the veins in small quantities and very dark in colour; at the same time it yields small amounts of an extremely tough and often gelatinous saliva, very rich in its specific constituents, and especially in mucus. The second species of nerve-fibres appears to cause widening of the vessels proceeding to the gland, for, when irritated, the blood flows in such quantity into the veins that they pulsate, and it is of a colour

¹ C. G. Mitscherlich, *Poggendorff's Annalen*, vol. xxvii. p. 320; Ludwig, *Lehrbuch der Physiologie*, vol. ii. p. 338; *Zeitschrift f. nat. Med.*, vol. i. (1851), p. 255.

² Oehl, *La Saliva umana*. Pavia, 1864. *Comptes Rendus*, 1864, vol. lix. p. 336.

³ v. Wittich, *Virchow's Archiv*, vol. xxxvii. p. 93; vol. xxxix. p. 184.

⁴ Nawrocki, *Stud. d. phys. Institut. zu Breslau*. Heft 4 (1868).

⁵ Owsjannikow and Tschiriew, *Bull. de l'Acad. Imp. des Sciences de St.-Petersbourg*, May 18, 1872; also, on the same subject, Grützner and Chtapowski, *Pflüger's Archiv*, vii. p. 522.

⁶ Bernard, *Comptes Rendus*, 1858, vol. xlvii. pp. 245 and 393; vol. lv. p. 341.

⁷ Eckhard, *Beiträge z. Anat. u. Phys.*, vol. i. p. 81; vol. ii. p. 205; vol. iii. p. 41.

almost as bright-red as that in the arteries; the saliva secreted under these circumstances is copious, and, as it contains but small quantities of specific constituents, very fluid. The fibres of the first kind run, to all the glands, in nerves of the sympathetic system. Those of the second kind arise in the facial and afterwards pass into the course of the trigeminus; viz. in the case of the parotid gland, through the nervous petrosus superficialis minor (of the facial), to the otic ganglion, and thence to the auriculo-temporal branch of the fifth (Bernard, Nawrocki¹); and, in the case of the submaxillary and sublingual glands, through the chorda tympani (of the facial) to the lingual branch of the fifth, whence, after a brief course, they pass, some directly, others through the submaxillary ganglion, to the gland (Bernard).

Even if it be assumed that the copious trigeminal-saliva secreted under great pressure deprives the gland of the same quantity of specific constituents in a unit of time as the scantier sympathetic saliva (Bernard), the vaso-motor effect would yet be insufficient to explain secretion; for the pressure in the glandular duct may rise higher than in the blood vessels, and secretion may be brought about, under nerve-stimulation, after the cessation of the blood-stream through the gland (Ludwig, Giannuzzi²). Some other mechanism, therefore, as yet unknown, must lie at the root of the process; and here the reader may be reminded of the assumed connection (according to Pflüger) of nerve-fibres with glandular cells. The following appearances (Heidenhain³) indicate yet more clearly a specific effect of secreting nerves: in the acini of those salivary glands, the secretion of which contain mucin, two species of cells are to be found: (1) nucleated, wall-less, 'protoplasm-cells,' containing much albumin, but no mucus. In many glands they lie thickly scattered about; in the submaxillary of the dog they form a crescent-shaped series on one side of the acinus, while in the cat they occupy the whole circumference. (2) Shining 'mucus-cells,' containing mucus enclosed in a cell-wall. After continued irritation of the secreting nerves, especially of those of the cerebro-spinal series, protoplasm-cells alone are found, undergoing rapid multiplication, while the remains of mucus cells are recognisable in the secretion. It is evident, therefore, that during secretion, a conversion of protoplasm-cells into mucus-cells through the 'mucin-metamorphosis' of their contents has taken place; the protoplasm-cells are replaced by the fission of those left, and the mucus-cells disintegrate. The cell-contents of the acini are, therefore, constantly in course of renovation, and a continuously stimulated gland resembles in appearance that of a recently-born animal. Some of the young protoplasm-cells appear to mingle with the secretion as salivary corpuscles. In the submaxillary gland of the rabbit, which yields a secretion containing no mucus, protoplasm-cells only are found. The buccal mucous glands resemble in their relations the mucus-yielding salivary glands. According to a later theory (Ewald⁴) regeneration of the glandular contents does not consist in destruction of the mucus-cells and their reformation out of protoplasm-cells, but simply in the liberation of the mucus contained in the former, whereby they again take on the appearance of protoplasm-cells. The temperature of salivary glands may be raised 1.5° C. during secretion (Ludwig and Spiess⁵).

¹ Nawrocki, *Stud. d. Phys. Institut. zu Breslau*, 1868, p. 125.

² Ludwig and Gianuzzi, *Ber d. k. sächs. Gesellsch. d. Wissensch. zu Leipzig*, 1865.

³ Heidenhain, *Studien des Phys. Institut. zu Breslau*, Heft 4 (1868), p. 1.

⁴ Ewald, *Centralblatt f. d. med. Wissen.*, 1870, p. 875.

⁵ Ludwig, *Lehrbuch*. vol. ii. p. 842.

As there exist poisons which paralyse the secretory fibres of the chorda tympani without interfering with those which cause vascular dilatation, *e.g.* atropia (Heidenhain¹), it is probable that the former are not identical with the latter.

The salivary glands, therefore, probably receive four different varieties of centrifugal nerve-fibres capable of influencing the secretion, viz. separate vaso-motor and separate secretory fibres in each of the two classes of nerves (cerebro-spinal and sympathetic) going to them.

Salivary secretion brought about by reflex irritation of nerves yields constantly a very fluid (trigeminal) saliva. In the case of the submaxillary gland the centre for this reflex action, when stimulation proceeds from the nerves of taste or from the stomach, is probably in the brain—the medulla oblongata—as irritation of that organ produces a secretion of saliva so long as the glandular nerves are intact (Eckhard). In the case of stimulations other than gustatory applied to the mucous membrane of the mouth the centre of reflection is the submaxillary ganglion. This is proved by the fact that, after section of the truncus tympanico-lingualis, stimulations of the former kind no longer produce any effect, while those of the latter kind operate as usual (Bernard). We must suppose, therefore, that the submaxillary ganglion is a centre presiding over secretion, which may be stimulated to reflex activity through certain fibres running from the tongue in the course of the lingualis, and leaving that nerve finally to reach the ganglion. On the contrary, the fibres coming from the brain, and conducting reflected impressions which originated in the gustatory nerves, reach the ganglion by way of the facial, chorda tympani and tympanico-lingualis, and probably simply traverse it (Bernard).

It is, moreover, worthy of remark that, on cutting away the submaxillary ganglion, with the exception of the fibres passing through it from the tympanico-lingualis, or on poisoning the blood flowing through the gland with curare, a continual secretion is induced, which can only be increased by the stimulation of sapid substances (Bernard). This 'paralytic' secretion appears also in the gland of the opposite side (Heidenhain). A continuous secretion, moreover, occurs if the tympanico-lingual trunk has been cut through for a long time; in which case the sympathetic fibres alone are able (in the manner before indicated) to modify the secretion. An explanation of this paralytic secretion has been sought partly in the supposed existence of inhibitory nerves, and partly (Heidenhain) in some effect of the stagnating secretion. The paralytic secretion soon ceases, in consequence of the degeneration of the glands.

The amount of saliva secreted in twenty-four hours has been variously estimated at from $\frac{1}{2}$ to 2 kilog. The fluid constituents of saliva, with the exception of the mucin, are probably for the most part reabsorbed in the alimentary canal (Chap. III.)

¹ Heidenhain, *Pflüger's Archiv*, vol. vi. p. 309.

3. Gastric Juice.

Gastric juice is the secretion of the tubular glands, which, closely packed and swollen inferiorly, crowd the gastric mucous membrane. Gastric juice is a thin, clear, colourless, acid fluid which is mixed in the stomach with gastric mucus. Its specific constituents are: (a) free hydrochloric acid; this may, without prejudice to the effect of the gastric juice, be replaced by lactic acid, which is generally formed in the stomach during digestion (Chap. III.): (b) a hydrolytic ferment *pepsin* capable of splitting up albuminous bodies. Pepsin has the property in acid solutions of quickly dissolving coagulated albuminous substances at the temperature of the body. Solution, preceded by swelling up of the albumin, takes place most rapidly under that degree of acidity which can produce the quickest swelling up (*e.g.* for the fibrin of ox, 0·8 to 1 grm. HCl per litre, Brücke). With the same quantity of acid, however, it takes place more quickly the more pepsin there is in the solution, until a maximum is reached, beyond which the solution cannot be hastened. A certain quantity of pepsin has the power of dissolving fresh amounts of albumin, if the acid used up be continually replaced. The changes which albuminous bodies undergo during solution are as yet little understood. At first they appear to retain their original properties. They are precipitable by heat (provided that, before being subjected to the action of the gastric juice, they had not been coagulated by heat, in which case the swelling up and solution generally take a longer time), and also, for some time, by neutralization with alkalies. They are therefore at this stage converted into syntonin. After a longer period they lose the power of being precipitated by heat, alcohol, mineral acids and certain metallic salts, and are called in this condition *peptones*. Peptones have, moreover, a far greater power of diffusion than ordinary albuminous solutions (Funke¹). Dissolved albuminous bodies undergo the same transformation under the influence of the gastric juice. Gelatin is, by the action of gastric juice, converted into an ungelatinizable modification. All these changes must, most probably, be regarded as hydrolytic decompositions. As a smaller amount of peptones is obtained, during continued pepsin-digestion, than corresponds to the albumin used, it would seem that peptones are capable of still further decomposition, the products of which are, however, yet unknown (Kühne²). Under the action of the gastric juice, even when neutralised, milk is firstly curdled and the precipitate of casein afterwards digested. It is supposed

¹ Funke, *Virchow's Archiv*, vol. xiii. p. 449; *Lehrbuch der Phys.* fifth ed. vol. i. p. 166.

² For Kühne's most recent views concerning the decomposition of albuminous substances, see a paper entitled 'Weitere Mittheilungen über Verdauungsenzyme und die Verdauung der Albumine,' *Verhandl. d. Naturhist. Med. Vereins zu Heidelberg*, 1876.

that pepsin quickly converts milk sugar into lactic acid ; milk, however, coagulates even when the gastric juice is alkaline. Processes of fermentation and putrefaction are generally hindered by the gastric juice.

The curdling of milk does not depend upon lactic acid fermentation, but upon a special ferment of the gastric juice, which has the property of precipitating casein ; a third ferment, which ultimately does lead to the promotion of lactic acid, acts so slowly that it cannot be concerned in the curdling. (Hammarsten, A. Schmidt.)

The active properties of the gastric juice are suspended by the same influences as deprive ferments of their activity (boiling, concentrated acids, many metallic salts, strong alcohol, &c.) Concentrated salt-solutions delay the solution of the albuminous bodies, as they hinder their swelling up. In the same manner solution is delayed if the swelling up be prevented by tying thread tightly round the pieces of coagulated albumin. Bile also retards solution, not only by neutralising the acid, but also by hindering the swelling up (Brücke¹), and precipitating the peptones (Bernard²).

It has been sought to explain the interference of bile with gastric digestion (Burkart) by the fact that a precipitation of glycocholic acid occurs on the addition of bile to acid gastric juice, the pepsin being supposed to be carried down mechanically in the process. It is urged, on the contrary (Hammarsten³), that bile which contains only taurocholic acid also destroys gastric digestion ; that, further, non-albuminous gastric juice is *not* precipitated on the addition of bile, and yet loses its digestive properties on admixture with that body. Pepsin is not destroyed in the process, but can be again isolated in an active condition. The power which bile possesses of preventing digestion depends principally upon the fact that it hinders the swelling up of the albuminous bodies ; it precipitates the peptones already formed, even when the fluid is decidedly acid (Brücke, Schiff). The prevention of the process of swelling up is said to depend upon the combination of the bile-acids with albumin (Hammarsten). Glycocholic acid does, however, possess the power (Burkart) of precipitating pepsin. The secretion of Brunner's glands also renders the gastric juice inoperative (Schiff).

Natural gastric juice is obtained from pathological, or (in the case of the lower animals) artificial gastric fistulæ ; and also by causing sponges attached to a string to be swallowed, and, after a time, withdrawn from the stomach. Artificial gastric juice is prepared by infusing fresh or dry gastric mucous membranes with water or (von Wittich⁴) glycerin, and then adding hydrochloric acid (0.1 p. c.) ; or, also, by dissolving pure pepsin in water and acid. Hydrochloric acid may be replaced by lactic acid (which in equal amounts is less effective), or by oxalic, phosphoric, or acetic acids, but the activity of the gastric juice is thereby diminished.

The gastric juice of the dog, free from saliva, contains, as the mean of a number of experiments, in 1,000 parts :—Water 973.1, pepsin (and peptone) 17.1, free hydrochloric acid 3.0, salts 6.8 (Bidder and Schmidt).

¹ Brücke, *Wiener Sitzungsber.* (1859), vol. xxxvii. p. 131, and 1861, vol. xliii. p. 601.

² Bernard, *Leçons de Phys. Exp.* (1856), vol. ii. p. 430.

³ Hammarsten, *Pflüger's Archiv*, 1868.

⁴ Von Wittich, *Pflüger's Archiv*, vol. v. 1872, p. 435.

Secretion.

The following has recently been made out with regard to the structure of the gastric glands (Heidenhain,¹ Rollett²). The glands contain two sorts of round cells: (1) the smaller, so-called 'Hauptzellen' (Heidenhain), or 'adelomorphous cells' (Rollett), which fill the greater part of all the glands, and are alone found in certain glands, occurring especially in the pyloric region (the 'gastric mucous glands' of earlier authors); (2) the larger, so-called 'Belegzellen' (Heidenhain), or 'delomorphous cells' (Rollett), which occur, almost without exception, only near the bottom of the glands at the sides. During secretion (in the process of digestion) the glands, and especially the smaller cells previously referred to, at first swell up strongly, and afterwards return to their former size (Heidenhain³). Pepsin is formed in the gastric glands, whence it can be obtained by water in the form of a neutral solution, or, more easily, by the action of dilute hydrochloric acid. It is probable that, during life also, it is extracted from the cells by some acid fluid. Nevertheless the glands themselves very seldom exhibit an acid reaction, while the surface of the gastric mucous membrane is covered with a strongly acid gastric juice. The acid is, however, formed in the glands; for, if the surface of the mucous membrane is neutralized by means of calcined magnesia, then washed with water and allowed to stand, an acid reaction again appears after some time (Brücke). It must be supposed, therefore, that the gastric glands form pepsin and an acid, but get rid of the latter (charged with pepsin) at once at the surface. The forces which effect these operations are not understood; nor is the origin of the free hydrochloric acid; for we can scarcely suppose that it results from the decomposition of some salt (perhaps calcium chloride, Smith) by lactic acid. Probably the simultaneous alkaline formation in the pancreatic secretion is closely connected with this acid formation (Meissner). The circumstance that the gastric mucous membrane yields far less pepsin to water and glycerin than it does to diluted acid or salt solutions is explained on the supposition that it contains a zymogen which only yields pepsin when it is treated with acids or salts; only the fundus of the stomach, which contains the delomorphous cells, forms the zymogen (Ebstein and Grützner). It has lately been surmised that the delomorphous cells [*i.e.* peptic cells of English writers] are merely a metamorphosed condition of the smaller adelomorphous cells (Herrendörfer). What part each of the two kinds of glandular cells takes in the formation of pepsin and acid is yet in dispute. While the formation of pepsin used to

¹ Heidenhain, *Archiv f. mikr. Anat.* vol. vi. 1870, p. 368.

² Rollett, *Untersuch. aus dem phys. Inst. in Graz*, 2.

³ Heidenhain, *loc. cit.*

be ascribed to the larger glandular cells, it has recently been maintained that the smaller variety are the pepsin-formers, because the latter more easily disintegrate under the influence of hydrochloric acid when warm than the former, and snippings from the surface of the gastric mucous membrane digest the more quickly the greater the number of the smaller kind of cells they contain (Heidenhain, Ebstein and Grützner¹). Others, on the contrary, hold to the former opinion, chiefly because the glands in the pyloric end of the stomach, which contain the smaller cells only, do not yield an infusion capable of digesting foods, if the secretion of the larger cells is absent (Friedinger,² von Wittich, Wolfhügel, opposed by Ebstein and Grützner, Klemensiewicz).

Secretion of gastric juice appears to occur only under the influence of the nervous system exerted in a reflex manner (see Saliva). It ceases when the stomach becomes empty; but recommences when it is filled with substances (food) which mechanically irritate it; and, probably also, on irritation of the mucous membrane of the mouth. The saliva which is swallowed seems to be concerned in this stimulation (Rollett). Secretion appears to be independent of the integrity of the nerves (vagi, &c.) supplying the stomach; the central organs, therefore, of a portion of the secretory nerves must be sought for in the walls of the stomach itself (Brücke, Ravitsch). During secretion a reddening of the mucous membrane occurs, and probably, therefore, a dilatation of the glandular vessels, similar to that which takes place in the secretion of saliva.

If the nerves be divided, a continual secretion of gastric juice is supposed to occur (H. Braun). The process of storing up the mucous membrane with pepsin or its zymogen, which appears to proceed side by side with the enlargement of the 'peptic cells,' increases when food is taken (Grützner); its dependence upon a supply of certain substances, such as dextrin [*substances peptogènes* of Schiff³], has not been confirmed.

The secreted gastric juice is, probably, for the most part, reabsorbed in the intestines (Chap. III.) Small amounts of pepsin are, therefore, found in various fluids of the body, *e.g.* in the parenchymatous juices of the muscles, in urine (Brücke). The acid of the gastric juice is neutralized by the alkaline intestinal juice. When the action of the latter is prevented, the urine becomes alkaline (Maly). No serviceable determination or estimation exists of the amount of gastric juice secreted.

¹ 'Ebstein und Grützner, 'Ueber den Ort der Pepsinbildung im Magen,' *Pflüger's Archiv*, 1872, vol. vi. p. 1.

² Friedinger, *Wiener Sitzungsber.*, 1871 (Oct.)

³ Schiff, *Leçons sur la Physiologie de la Digestion*, vol. ii. p. 200, *et seq.*

4. *Bile.*

Bile is a neutral or weakly alkaline, mostly viscid, bitter fluid, varying in colour from yellow, brown, or green to black. Its specific constituents (apart from the mucus which originates in the gall-bladder and ducts) are:—(1) the sodium salts of two conjugate acids (so-called 'bile-acids'), viz. glycocholic acid (called also cholic acid) and taurocholic acid (called also choleic acid). The former is compounded of nitrogenous glycocine and non-nitrogenous cholic acid, the latter of taurine (which contains nitrogen and sulphur) and cholic acid; (2) cholesterin, held in solution by the salts of the bile-acids; (3) products of decomposition of lecithin, viz. choline or neurine, and glycerin-phosphoric acid; (4) urea (Popp); (5) colouring matters, especially one of a reddish-yellow colour, bilirubin (cholepyrrhin, bilifulvin); another of a green colour, biliverdin, perhaps only a derivative of the former; (6) small quantities of fats and soaps; (7) a sugar-forming ferment (J. Jacobson, von Wittich¹); (8) sugar (Naunyn).

Bile may be obtained from the gall-bladder after death; and, during life, in the lower animals by means of artificial biliary fistulæ, which may, at the same time, be used to determine the amount secreted in a given time. The colour of bile varies much under different physiological, and still more under different pathological, conditions, and in different classes of animals. In the air yellow bile becomes green through the oxidation of bilirubin to biliverdin. The bile of vegetable-feeding animals is green while in the gall-bladder. The salts of the bile-acids may be easily obtained by evaporating bile, extracting with absolute alcohol, decolourizing the extract by means of animal charcoal, and adding absolute ether. When prepared in this manner, they are obtained in the form of a resinous precipitate, which becomes crystalline on being kept in a mixture of alcohol and ether ('crystallized bile'). The two bile-acids are present in various proportions; in man, amphibia, and fishes, taurocholic acid predominates, as also in many mammals and birds: in others (*e.g.* in pigs, kangaroos), it is glycocholic acid which predominates. The cholic acid contained in the bile-acids is replaced in various animals, by other allied acids (p. 18), *e.g.* in the goose by chenocholic acid, in the pig by hyocholic acid, in guano by guanogallic acid; and the bile-acids bear different names accordingly (taurochenocholic acid, hyoglycocholic acid). The bile-acids rotate the plane of polarization to the right, cholesterin to the left (Hoppe-Seyler).

Human bile contains in 1,000 parts, water 822·7–908·1; salts of the bile-acids 107·9–56·5 (some estimates are lower than these, Trifanowsky, Socoloff); fat and cholesterin 47·3–30·9; mucin and colouring matters 23·9–14·5; ash 10·8–6·3 (v. Gorup-Besanez).

Secretion.

The formation of bile takes place in the so-called *lobules* (*acini*) of the liver. Each acinus receives, like the whole liver, arterial blood, which is brought by the *hepatic artery*, and venous blood, which is conducted through the *portal vein* from the capil-

¹ V. Wittich, *Pflüger's Archiv*, vol. vi. 1872, p. 181.

laries of the stomach, intestine, pancreas and spleen; and each furnishes venous blood to the *hepatic vein*.

The terminal branches of the portal vein (*interlobular veins*), and of the hepatic artery, which lie at the periphery of the lobule, are connected with the initial branches of the hepatic vein (*intra-lobular veins*), which start from the centre, by a close, interlacing capillary network, whose meshes are crowded by the large, round, glandular *cells* of the liver. These liver-cells are so arranged (Hering) that they form the wall of the finest gall-passages, often as few as two only occurring in a transverse section. These passages open into an interlobular network surrounding the acini, whence springs the *hepatic duct*, which, after giving off a lateral branch, the *cystic duct*, to a reservoir, the *gall-bladder*, opens into the duodenum as the *ductus communis choledochus*. The blood of the portal vein, which has previously traversed one capillary system, and which is now for the second time distributed over an enormous vascular area, must flow extremely slowly in the capillaries of the liver.

Bile-formation takes place continually. It would seem that, during the intervals between periods of digestion, the secretion is conveyed through the cystic duct to the gall-bladder, and there stored up; but that, during digestion, it is poured, both directly from the liver, and also from the gall-bladder, into the intestine. The formation of the specific constituents takes place in the liver-cells. That these constituents are not simply separated from the blood is shown by the fact that, neither under ordinary circumstances, nor when secretion is prevented (by extirpation of the liver) can they be detected in the blood flowing to the liver.

On the contrary, they rapidly appear in the blood if the outflow of the bile from the liver is prevented by the stoppage of the excretory duct, and the pressure in the gall-passages by this means raised; a very slight pressure is all that is required to effect this return into the blood; biliary colouring matters, cholic, glycocholic, and taurocholic acids, may then be detected in the urine (Hoppe-Seyler), and the first colours the urine brown, and the skin and mucous membranes yellow—Jaundice. Other colouring matters also, which appear in the gall-passages under pressure, are re-absorbed and colour the mucous membranes, &c. The acini themselves do not become coloured under these circumstances; nor is the bile coloured, which is secreted by them at the same time; absorption does not, therefore, in the liver take place in the acini, but in the gall-passages (Heidenhain).

It is uncertain from which of the two kinds of blood flowing into the liver the materials for the preparation of bile are chiefly derived. According to some investigators (Oré, Frerichs, and others), ligature or obliteration (Kottmeyer) of the hepatic artery suspends the secretion of bile, while that of the portal vein has no such result. Other researches (Schiff) have led to exactly opposite results. According to recent researches (Cohnheim and Litten) the hepatic artery only supplies the hepatic ducts and the connective tissue with blood; these capillary systems empty into the interlobular veins, the portal vein alone supplying the acini.

Comparative examinations of blood flowing into and out of the liver have merely approximately disclosed the nature of the substances which are retained in the liver and there converted into the

constituents of bile. Analysis of blood from the portal and hepatic veins shows that, apart from the appearance of sugar in the latter (Chap. V.), hepatic venous blood contains less water, albumin, fibrin, fats, blood-colouring matter and salts, but more blood corpuscles (Chap. V.) than portal blood, which, especially after digestion, is very rich in fats (Lehmann, C. Schmidt). The high temperature of the gland and of hepatic venous blood shows that active oxidation goes on during secretion.

Of the more special chemical changes which take place during secretion, the most probable is the formation of the biliary colouring matters from blood-colouring matter, which is based upon the identity (Virchow, Valentin, Jaffe), or at least the strong resemblance (Städeler and Holm) of bilirubin and hæmatoidin. Some maintain, also, the origin of cholic acid and sugar from fats, the glycerin, according to various hypotheses, yielding sugar, and the fatty acids, cholic acid; but the existence of such processes is as yet unsupported by facts. The processes of decomposition which take place during digestion may possibly account for the origin of glycocine and taurine; and the further syntheses in which they take part may have their seat in the liver. The glycocine of the liver may be conjugated with other acids than cholic acid, *e.g.* with benzoic acid, to form hippuric acid (see under Urine).

The amount of bile secreted, which it is impossible to estimate exactly, varies between about 160 and 1,200 grms. in twenty-four hours (as Ludwig has estimated from the data of others). It depends to a large extent upon the food taken. It is increased by ingestion of water (in which case the bile is more watery), by an animal diet, and, to a less extent, by a vegetable diet also. Fatty foods do not at all increase the amount secreted; and starvation diminishes it considerably. The maximum of secretion is reached several hours after the ingestion of food, and it occurs the later the more plentiful the meal has been (Béchamp). The influence of the nervous system upon the formation of bile is little known; irritation of the vaso-motor nerves of the liver, especially of the splanchnics, diminishes secretion (Heidenhain, J. Munk).

Other substances may be found abnormally in the bile, which have been taken into the body along with the food, and are being voided by this way. Heavy metals, especially, are said to find their way into the liver and the bile. Copper and lead occur somewhat regularly in the liver.

Concerning other functions of the liver, see Chapter V.

Separation.

The outflow from the liver of the bile already formed is occasioned probably by the mechanical pressure exerted by the secretion, assisted by the compression of the liver during inspiration. The amount of bile collected from fistulæ is, therefore, diminished during the slow respiration which follows section of the vagi (Heidenhain). The evacuation of the gall-bladder and the larger gall-passages, however, is probably brought about by the contrac-

tion of their smooth muscular fibres, which takes place simultaneously with the movements of the intestine (Heidenhain).

Such contractions may be artificially induced by stimulating the spinal cord. The first effect of this irritation is an expulsion of bile, of which, however, the flow soon diminishes, owing to the simultaneous irritation of vaso-motor nerves; both the nerves supplying the muscular coats of the biliary passages and the vaso-motor nerves are contained in the splanchnics.

As animals with biliary fistulæ quickly grow lean, provided they are prevented from devouring the bile which escapes, it is supposed that the greater portion of the bile is reabsorbed in the intestines. The ultimate destination of the reabsorbed biliary matters is, however, not known; nor have the other circumstances, which help to explain the starvation of the animals from which the biliary secretion is removed, been completely eliminated from the question. Moreover, in the normal condition, all the biliary substances are found in the fæces in considerable quantities—the colouring-matters which colour the fæces, bile-acids, mucus, cholesterin, &c. The bile-acids, especially taurocholic acid, undergo in the lower part of the intestinal tube a hydrolytic decomposition (Chap. III.); there being found in the fæces, therefore, glycocholic acid, cholic acid, and their anhydrides, choloidic acid and dyslysin (Hoppe-Seyler). The reabsorption of the specific constituents of bile is, therefore, yet doubtful.

Unlike all the other secretions connected with the digestive apparatus, bile is probably of no importance in digestion proper (*i.e.* in the preparation of food for absorption).

[This statement is perhaps too absolute. The researches of Kühne lead us to the inference that the bile aids pancreatic digestion by co-operating in the neutralization of the gastric juice, the pancreatic ferment (trypsin) being not merely inactive in an acid fluid which contains pepsin, but being actually destroyed by it.]

The one property it possesses, which is of value for that purpose, viz. that of emulsionising fats, is shared by it with other secretions which possess it in a far higher degree (pancreatic juice, and, perhaps, intestinal juice). Solutions of peptones are precipitated by bile; a circumstance the importance of which will be spoken of in the next chapter. The importance of bile physiologically appears to be chiefly in regard to the absorption of fats (Chap. III.) Bile (and the salts of the bile-acids), for instance, renders possible both filtration of fats through membranes under slight pressure, and diffusion between fats and watery solutions (von Wistinghausen), probably because it occasions the simultaneous imbibition of both (a condition of diffusion), in the form of soapy solutions. It renders easier, also, the passage of fats through narrow (capillary) tubes. Bile is also said to induce contraction of the muscular fibres of the villi (Chap. III.)

(Schiff), and thus, again, to assist in the absorption of fats. It appears moreover to prevent putrefactive decomposition of the contents of the intestine. (Its power of preventing butyric fermentation has been directly determined by Paschutin.)

In accordance with what has been said above, when bile is suffered to escape through a fistula, there occurs no essential disturbance of the digestive processes, but only (1) prevention of the absorption of fats (as indicated by the fat contained in the fæces, and the absence of fat in the chyle); (2) colourless, ill-odoured, hard fæces; (3) at the same time excessive hunger on the part of the animal; (4) the endeavour on the part of the animal to make up for the deficient absorption of fat by increased consumption of hydro-carbonaceous foods (Chapter VI.)

5. *Pancreatic Juice.*

The pancreatic juice secreted in the racemose pancreas, whose structure resembles closely that of the salivary glands, is a strongly alkaline, clear, very tough, colourless fluid, coagulable by heat. Its specific constituents are (1) several albuminous bodies coagulable by heat, which are scarcely distinguishable from albumin itself, and to which many observers ascribe the ferment-action of the secretion (pancreatin). According to others (Danilewsky) the ferments of the pancreatic secretion are special bodies. (2) Several hydrolytic ferments (see below) capable of separation one from another. (3) Leucine and other products of decomposition of albuminous bodies.

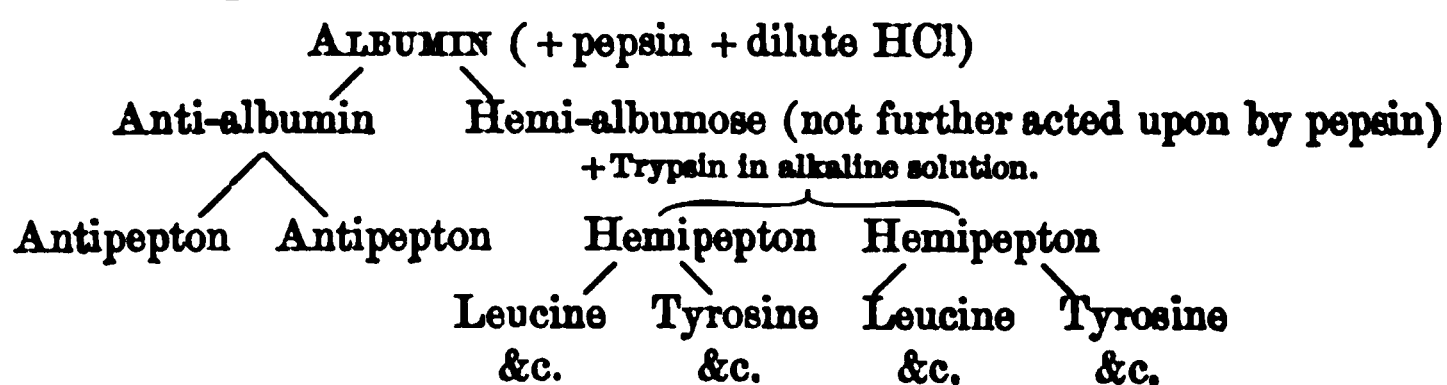
Pancreatic juice may be obtained by means of artificial fistulæ; and an artificial juice may be made by infusing the glandular substance in water or glycerin.

The pancreatic juice has, by virtue of the ferments it contains, three well-marked properties which render it very important in indigestion: (1) It converts starch-mucilage into dextrin and sugar more powerfully than saliva from the mouth (Bernard). (2) It decomposes neutral fats very quickly, in such a manner that, in the presence of water, glycerin and free fatty acids are formed (p. 29); the latter then partly combine with the alkali of the pancreatic juice to form soaps, while the excess causes an acid reaction. With the decomposition is connected an emulsification of the fats (Bernard), which is probably brought about by the products of decomposition themselves (Brücke). (3) Coagulated albuminous bodies are dissolved by the pancreatic juice, as also is gelatin (Corvisart). The ferment, pancreatinin (or trypsin, Kühne) is only active in alkaline solutions (compare in this respect pepsin), and does not lead to a preliminary swelling up of the matters digested. The fluid in which the dissolved proteids are contained agrees in its characters with solutions of peptones (Kühne). After the lapse of some time, however, the peptones found are further decomposed (Kühne), and there appear leucin, tyrosin, aspartic and glutamic acids (Radziejewski and

Salkowski, v. Knieriem), besides unknown extractive matters, amongst which is Indol, $C_{16}H_{14}N_2$, which is coloured violet by chlorin, and which possesses an unpleasant fæcal odour.

[The proteolytic formation of the pancreas is from the foregoing facts proved to be a very different body from that contained in the gastric juice. The conditions of its activity are different, alkalinity being as essential to it as is acidity to the proper activity of pepsin, and the products of that activity are different also; besides which, as far as can be made out, trypsin possesses a very different chemical composition, being in all probability proteid in nature. Kühne explains the different action of pepsin and trypsin on the proteid bodies by assuming that these bodies are capable of being decomposed up to a certain point by both ferments. Every proteid, according to Kühne, can be decomposed into bodies belonging to two groups, termed respectively the anti- and hemi-group; thus albumin, under the influence of either pepsin or trypsin, is decomposed into bodies to which Kühne gives the name of Anti-albumin and Hemi-albumin. The former, by the continued action of pepsin, may be converted into so-called antipeptone, the characteristic of this body being that it cannot, by the action of either of the digestive ferments under consideration, be further split up; pepsin can, however, exert no further action on the Hemi-albumose; if, however, subjected to the action of trypsin, that body splits up into leucine, tyrosine, &c.

Kühne's views will be better understood by a glance at the accompanying schema of the digestive decomposition of albumin:



A characteristic of tryptic digestion which distinguishes it from peptic digestion has been referred to in the text, and is of importance, to wit,—proteids, when subjected to the action of pepsin and hydrochloric acid, always swell up and become transparent, and it is only after this preliminary stage that solution commences; when digested by trypsin they do not, however, swell up in this fashion, the body which is being dissolved presenting an opaque and eroded surface.]

The leucine which is contained in the pancreatic juice is a product of the action of the juice upon the proteids which it contains; the rose-colouration produced by the action of chlorine on the pancreas (Tiedemann and Gmelin) is to be explained in a similar manner. The formation of Indol appears to be the result of a process of decomposition, for it is invariably associated with the development of organisms (Hüfner, Kühne), and does not occur in the presence of such antiseptic agents as salicylic acid.

When gelatin is digested by trypsin there occurs decomposition into leucine, glycine, ammonia, but no indol is formed (v. Nencki). Even alkaline albuminate is digested by pancreatic juice, though more slowly than fibrin (Senator). The gas generated during pancreatic digestion, if putrefaction be hindered, consists entirely of carbonic acid, and this, too, is absent if oxygen be kept away: when putrefaction sets in, hydrogen, marsh gas, nitrogen, &c., are liberated (Hüfner, Kunkel, and others).

Besides the fats, other glycerin ethers are decomposed by the pancreatic juice, as monobutylin (Berthelot), acetic ether (Heritsch).

It is worthy of remark that all the above-mentioned actions of the pancreas

are the same which are induced by boiling with mineral acids (compare p. 27). Pepsin hinders the action of trypsin (Kühne.) [It has been shown by Kühne that pepsin in acid solution actually destroys trypsin; trypsin in alkaline solution does not possess the converse power of destroying pepsin, which, however, is altogether inactive in an alkaline fluid.]

The pancreatic juice of the dog contains 91 per cent. of water, 8.2 per cent. of organic matter, 0.8 per cent. of ash (Bernard).

Secretion.

The secretion of pancreatic juice probably never takes place without nervous stimulation (as is the case with saliva). It is usually very slight, but increases much during digestion. That the specific constituents of the secretion are formed in the glandular cells is proved by (1) the activity of an infusion of the glandular substance, and (2) the presence of cell-fragments in the secretion (Donders). It may be assumed, therefore, that the constituents become free in this case also by the disintegration of the cells. Increased secretion is constantly accompanied by increased circulation, and reddening of the gland (Bernard¹). We may, therefore, surmise some vaso-motor effect of the nerves, as is the case with the salivary glands.

The nerves affecting this secretion are unknown; they appear to be called into action reflexly by stimulation of the gastric mucous membrane, just as are those of the salivary glands on stimulation of the mucous membrane of the mouth (Ludwig²); hence the secretion of the gastric and pancreatic juices occurs simultaneously (Bidder and Schmidt³). Irritation of the medulla oblongata increases the flow, probably only by inducing contraction of the duct (Landau). Irritation of the central end of the vagus stops the secretion (N. O. Bernstein⁴); the same stoppage occurs during vomiting (Weinmann⁵, Bernard⁶). The relative amount of solid constituents is inversely proportioned to the rapidity of secretion (Weinmann); that of salts, however, is pretty constant, and is the same as in blood-serum (N. O. Bernstein).

The quantity of pancreatic juice secreted cannot be accurately estimated by means of fistulæ, because the pancreas has two anastomosing excretory ducts. The ultimate destination of the secretion is probably the same as that of saliva and gastric juice.

6. *Intestinal Juice.*

Intestinal juice (*Succus entericus*) is the secretion poured out by the tubular glands of Lieberkühn, which are present in all parts of the intestine. It was not possible until quite recently to obtain pure intestinal juice. The method now adopted is as follows (Thiry⁷): An animal is taken and a portion of the intestine,

¹ Claude Bernard, *Leçons de Phys. Expl.*, 1856, vol. ii. pp. 170–377.

² Ludwig, *Lehrbuch d. Phys.* vol. ii. p. 354.

³ Bidder and Schmidt, *Die Verdauungssäfte*, p. 240.

⁴ N. O. Bernstein, *Ludwig's Arbeiten*, 1870, p. 1.

⁵ Ludwig und Weinmann, *Zeitsch. f. rat. Med. N. F.*, vol. iii. p. 247.

⁶ Bernard, *l.c.* p. 226.

⁷ Thiry, *Wiener Sitzungsber.*, vol. I. Part I. p. 77.

still connected with the mesentery, is separated from the rest. The two ends of the remaining portion are made to unite, the animal continuing to live, but with an intestine somewhat shortened. The portion separated from the rest is closed at one extremity, while the other is stitched to the sides of the wound in the abdomen. As the nutrition of the piece of intestine has not been interfered with, secretion will take place as usual, and the intestinal juice will be poured out at the open end.

The juice so obtained is a thin, bright yellow, strongly alkaline, albuminous fluid. It acts as a ferment only on fibrin, which it quickly dissolves (it does not dissolve other coagulated albuminous bodies, Thiry). Nothing is certainly known concerning its chemical constituents.

Under ordinary circumstances secretion is almost quiescent; but under the stimulation of mechanical irritation of weak acids, it may be largely increased (13 to 18 grms. hourly from a surface of 100 sq. cm.)

Formerly an impure intestinal juice was obtained through intestinal fistulæ by the removal of the food, or by introducing sponges into the intestines, or by preventing the admixture of the other secretions which are poured into the intestine. According to an older view, which has been supported in part in recent times, intestinal juice acts upon starch (Schiff, Quincke¹), and upon fats (Schiff²), like the pancreatic secretion, but somewhat more slowly. The ferments extracted from the intestinal mucous membrane by means of glycerin do not possess the power of digesting albumin, although they can convert starch into sugar. The glands of the large intestine are unable to bring about the latter operation (Eichhorst,³ Costa).

The intestinal juice of the dog contains 97·6 per cent. of water, 0·8 per cent. of albumin, 0·7 per cent. of other organic matters, 0·9 per cent. of ash (Thiry).

The acinous glands of Brunner of the duodenum yield a viscid secretion which has been little investigated, and which, upon the ground of anatomical analogies, was once compared with mucus, then with pancreatic juice, lately by Grützner with the secretion of the pyloric glands: even were pepsin formed in these glands it could exert no action on account of the alkalinity of the intestines and the bile.

2. RESPIRATORY SECRETIONS.

The lungs may be regarded in structure and function as a racemose gland with a gaseous secretion, the excretory duct of which is the trachea. As will be explained in Chap. IV., the forces which effect the separation of carbonic acid at the lungs are by no means thoroughly understood.

The numerous mucous glands which are scattered about the air passages, from the nasal opening in the face to the smaller bronchial tubes, yield a fluid mucus. The glands are racemose and possess

¹ Quincke, *Archiv f. Anat. u. Phys.*, 1868.

² Schiff, *Il Morgagni*, 1867, No. ix.; *Centralblatt*, 1868, No. xxiii.

³ Eichhorst, *Pflüger's Archiv*, vol. iv.

pavement-epithelium; the smallest of them are, however, more tubular, and are provided with cylindrical epithelium. The same remarks apply to this secretion as to that of the mucous glands of the alimentary apparatus. The mucus is apparently secreted only in small quantities, and the excess is removed from the body, by an arrangement which will be spoken of hereafter (Chap. IV.)

3. URINARY SECRETION.

The urine secreted in the kidneys is a true excretion, the removal of which from the organism is necessary, as it is of no further use. It serves to carry out of the body certain ultimate products of the oxidation of nitrogenous substances, as well as the excess of water. The products of oxidation are separated along with salts in the form of watery solutions.

Urine is a clear, transparent, amber-coloured, and slightly acid fluid, with a bitter saline taste and an aromatic odour (specific gravity 1.005—1.030). A little mucus from the mucous glands of the excretory ducts (especially of the bladder) is usually mixed with it. Its specific constituents are:—1. Urea, the chief ultimate product of the oxidation of nitrogenous bodies. 2. Uric acid, existing in the form of neutral urates of the alkalies. 3. Hippuric acid in very varying amounts; it may, indeed, be absent altogether. Of the organic constituents the above three are the most important; further: 4. Creatinine. 5. Xanthine. 6. Sarcine (Hypoxanthine); 7. Ammonia, both free and in salts, amongst which is ammonium-oxalurate. 8. Urinary colouring matters: urobilin, urohæmatin, occasionally indigo blue. 9. Indican. 10. Grape sugar (Brücke, denied by some). 11. Oxalic acid, in salts; 12. Inorganic salts, especially sodium chloride, acid sodium phosphate, sodium sulphate, carbonates, and in addition to salts of the alkalies those of calcium and magnesium. 13. Water. 14. Gases: oxygen, carbonic acid, and some nitrogen (Morin, Pflüger).

Which of the above-mentioned specific constituents of urine are most extensively represented seems to depend upon the kind of food taken. In flesh-eating mammalia urea is present, as in man, in largest amount; very little uric acid and hippuric acid being found. In the urine of vegetable-feeders but little urea and no uric acid are present, while hippuric acid abounds. Dietetic changes effect variations in the urine. Human urine also varies with the food ingested (see below), hippuric acid, especially, increasing with the increase of vegetable food taken, and disappearing when animal food alone is eaten. The urine of birds, scaled amphibia, insects, &c., which becomes solid immediately after evacuation, contains, on the contrary, an excess of uric acid or urates; that of birds contains also urea, creatine, albumin, &c. (Meissner).¹

Amongst the constituents of the urine which do not occur constantly, which are present in minute quantities, or the presence of which is doubtful, are to be mentioned the following: Alloxan, allantoin, taurine, cystine, leucine, tyrosine,

¹ Meissner, *Zeitschrift. f. rat. Med.* 1868, pp. 144–223.

a higher homologue of urea $\text{H}_2\text{N.CO.CH}_2\text{CH}_2\text{CH}_2$ (Baumstark¹), potassium sulphocyanide (Külz), phenol (monoxybenzene, especially after vegetable food and in the herbivora; Städeler; see below), pyrocatechin (dioxymethylene, also found chiefly after vegetable food; Ebstein and Müller,² Baumann³; see further), succinic acid (Meissner), hyposulphurous acid (in carnivora, Schmiedeberg). Free phenol is not present in urine, but it is formed by the action of acids upon a more complex body (Buliginsky); this substance may be phenyl-sulphonic acid ($\text{C}_6\text{H}_5\text{O.SO}_2\text{OH}$), and similarly pyrocatechin may in part be combined (Baumann). It has even been lately surmised, in reference to indican, that it is no glucoside, but a conjugate sulpho-acid (Baumann).

Many substances ingested with the food, or taken as drugs, reappear partly unaltered in the urine, *e. g.* most metallic salts, alkaloids, colouring matters. Other bodies appear in a more oxidized form; especially is this the case with the alkaline salts of many organic acids (lactic, succinic, acetic, citric, and malic acids), which appear as alkaline carbonates and render the urine alkaline (Wöhler⁴); similarly benzol appears as phenol (Schultzen and Naunyn), indol as indican (Jaffé⁵), uric acid in part as allantoin (Salkowski). Substances which are capable of complete oxidation do not cause the appearance of special constituents in the urine. Many substances combine in their passage through the organism with products of tissue changes (water being eliminated in the process), and the resulting compounds appear in the urine; such compounds are formed in the cases of glycine, carbamic acid, sulphuric acid, perhaps also cyanic acid. The most important fact of the kind with which we are acquainted is the passage of ingested benzoic acid into the urine as glyco-benzoic acid (hippuric acid) (Wöhler⁶).

The following bodies, like benzoic acid, reappear in the urine as hippuric acid: benzylaldehyde (oil of bitter almonds), cinnamic acid (phenylacrylic acid $\text{C}_9\text{H}_8\text{O}_2$), chnic acid ($\text{C}_7\text{H}_{12}\text{O}_6$); on the other hand gallic acid ($\text{C}_7\text{H}_6\text{O}_5$), which is so closely allied to the last-named bodies, passes uncombined into the urine, and an anhydride of this body, viz. tannic acid ($\text{C}_7\text{H}_{10}\text{O}_9$) appears in the urine, after undergoing hydrolytic decomposition, as gallic acid ($\text{C}_{14}\text{H}_{10}\text{O}_9 + \text{H}_2\text{O} = 2\text{C}_7\text{H}_6\text{O}_5$). Substituted benzoic acids, *e. g.* chlorobenzoic acid, nitrobenzoic acid, salicylic acid (one of the oxybenzoic acids), anisic acid (a methoxybenzoic acid), form corresponding substituted hippuric acids (chlorhippuric acid, salicyluric acid, anisuric acid, see p. 41).

The hippuric acid in the urine of vegetable-feeders is formed most probably out of some vegetable substance resembling benzoic acid taken into the body as food; the glycocine necessary for its formation is derived from the liver (Kühne and Hallwachs⁷). The vegetable substance is probably the cuticular substance of plants which appears most to resemble chinovic acid in composition (Meissner

¹ Baumstark, 'Ueber eine neue Verbindung aus dem Harne.' *Liebig's Annal.* Vol. clxxiii. pp. 342-355.

² Ebstein u. Müller, 'Vorkommen von Brenzcatechin im Urin eines Kindes.' *Archiv. f. Anat. u. Physiol.* Vol. lxiii. pp. 554-561.

³ Baumann, 'Ueber das Vorkommen von Brenzcatechin im Harne.' *Pflüger's Archiv.* Vol. xii. pp. 63-68.

⁴ Wöhler, *Tiedemann's Zeitschrift für Physiologie.* Vol. i. p. 305.

⁵ Jaffé, 'Ueber den Ursprung des Indicans im Harne.' *Centralbl. f. d. med. Wissenschaft* 1872, No. 1.

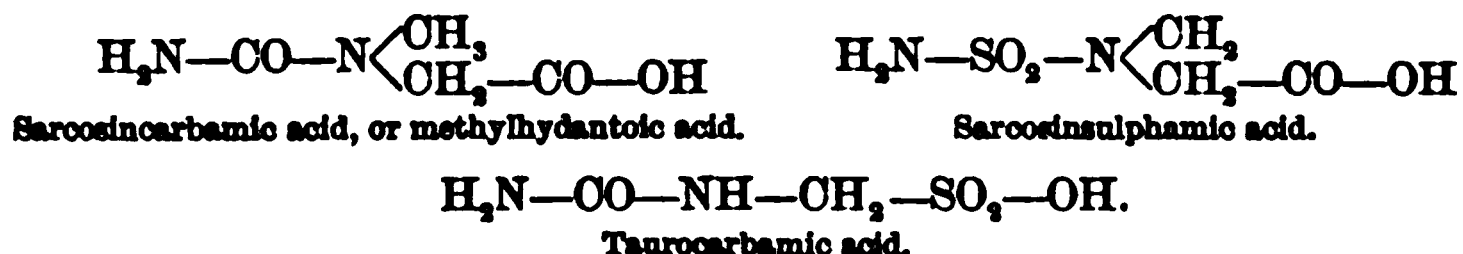
⁶ Wöhler, *Tiedemann's Zeitschr. für Physiol.* Vol. i. p. 305.

⁷ Kühne u. Hallwachs, *Virchow's Archiv.* Vol. xii.

and Shepard¹); for those portions of plants which possess no cuticular substance (e.g. underground portions, huskless grains of corn) yield no hippuric acid.

In opposition to this surmise it is, however, alleged that hay treated with diluted sulphuric acid yields no hippuric acid (Weiske). It is possible that other bodies similarly distributed, and allied to benzol, are the sources of hippuric acid (Nencki).

With carbamic acid (p. 36) the following bodies are said to unite: sarcosine (Schultzen²; this is, however, denied by others) and taurine (Salkowski³). Both these bodies are said to unite themselves also with the perfectly analogous sulphamic acid ($\text{NH}_2\cdot\text{SO}_2\cdot\text{OH}$); there are formed in this way, sarcosincarbamic acid or methylhydantoic acid ($\text{C}_4\text{H}_8\text{N}_2\text{O}_3$), sarcosinsulphamic acid ($\text{C}_4\text{H}_8\text{N}_2\text{SO}_4$), taurocarbamic acid ($\text{C}_5\text{H}_8\text{N}_2\text{SO}_4$).



It is stated that other bodies, such as phenol, pyrocatechin, oil of turpentine, form conjugated compounds with sulphuric acid, which have been already referred to (Baumann⁴); the formation of indican from indol is looked upon as a process of the same kind (refer to what was stated previously). As carbamic acid has not been determined with certainty to exist in the organism [see page 36], we may consider cyanic acid ($\text{ON}\cdot\text{OH}$) to be the body which conjugates itself in the above-mentioned cases; cyanic acid only differs from carbamic acid by containing H_2O less, and at any rate it yields artificially with sarcosine and taurine methylhydantoin and taurocarbamic acid (Baumann,⁵ Salkowski⁶).

When glycine and leucine are taken into the system they appear as urea in the urine (Schultzen and Nencki⁷); this is not the case with tyrosine (Küssner); ammoniacal salts and amides, e.g. aspartic acid and asparagin, form urea (v. Knieriem⁸); even these processes may be looked upon as conjugations with carbamic or cyanic acids; in favour of such hypothesis is the fact that when these bodies are introduced into the organism the rate of decomposition of the proteids of the body increases (Salkowski⁹).

The colour of urine varies with its state of concentration: it is darkest in the concentrated morning-urine ('urina sanguinis'), and lightest in that passed after the plentiful ingestion of fluids ('urina potus'). The acid reaction results for the most part from

¹ Meissner u. Shepherd, *Zeitschr. f. rat. Medizin.*

² Schultzen, 'Entstehung des Harnstoffs im Thierkörper.' *Ber. d. deutsch. Chem. Gesellsch.* Berlin, 1872, p. 578.

³ Salkowski, 'Ueber die Taurocarbaminsäure und deren Synthese.' *Ber. d. deutsch. Chem. Gesellsch.* Berlin, 1878, vol. vi. pp. 744, 1312 and 1191.

⁴ Baumann, *Pflüger's Archiv.* Vol. xii. p. 69; vol. xiii. p. 285.

⁵ Baumann und Hoppe-Seyler, 'Ueber Methyl-hydantoinsäure.' *Ber. d. d. Chem. Gesellsch.* Vol. vii. p. 84.

⁶ Salkowski, 'Einwirkung von Kaliumcyanat auf Tarkosin (Methylhydantoinsäure).' *Ber. d. d. Chem. Ges.* Vol. vii. p. 116.

⁷ Schultzen u. Nencki, *Zeitschr. f. Biolog.* Vol. viii. p. 188.

⁸ V. Knieriem, 'Beiträge zur Kenntniss der Bildung des Harnstoffs im thierischen Organismus.' *Zeitschr. f. Biol.* 1874, vol. x. pp. 263-294.

⁹ Salkowski, 'Ueber die Vorgang der Harnstoffbildung im Thierkörper und den Einfluss der Ammoniaksalze auf denselben.' *Zeitschr. f. physiologische Chemie.* 1877, vol. i. pp. 1-59. See also Schmiedeberg, 'Ueber das Verhältniss des Ammoniaks und der primären Monaminbasen zur Harnstoffbildung im Thierkörper.' *Archiv. f. exp. Path. u. Pharmacol.* 1877.

the contained acid sodium phosphate (Liebig). That urine contains no free acid is proved by the fact that it gives no precipitate on the addition of sodium hyposulphite (Huppert). Sometimes normal urine is alkaline, namely, after caustic alkalis, or alkaline carbonates, or salts of vegetable acids have been taken into the stomach. (The latter, viz. the salts of the vegetable acids, having undergone oxidation, appear in the urine as carbonates, which have an alkaline reaction, Wöhler.¹)

On standing, urine forms gradually a precipitate of acid urates or free uric acid. Simple cooling cannot be the cause of this, for, on again heating to the temperature of the body, the sediment is not completely redissolved. We must, therefore, suppose an acid-formation to take place, by a species of fermentation, due probably to the influence of the mucus which is present ('acid fermentation,' Scherer). After some time (which is shorter the higher the temperature) decomposition sets in, owing to the organic germs which the urine receives from the atmosphere; in this process urea is converted into ammonium carbonate, the reaction becomes alkaline ('alkaline fermentation'), a putrefactive odour appears, and precipitates of ammonium urate, ammonio-magnesium phosphate, &c., are formed, with the development of fungi and infusorians. It has lately been questioned whether the ferment which leads to the alkaline fermentation is an organised ferment.

[Inasmuch as the percentage composition of the urine is continually being affected by the very varying state of activity of other organs, by the amount of food which is being taken, &c., it is impossible to give more than a very approximate statement of its average composition. The following table (Vogel) fairly enough represents, however, the composition of the mixed urine of twenty-four hours of an average man :—

Specific gravity, 1020.					
Water in 1000 parts	960
Solid residue	40
Urea	23·3
Uric acid	0·5
Sodium chloride	11·0
Phosphoric anhydride	2·3
Earthy phosphates	0·8
Sulphuric anhydride	1·3
Ammonia	0·4]

Secretion.

The secreting apparatus of the kidneys (for a more detailed account of the structure of which refer to 'Manuals of Histology') consists of the *tubuli uriniferi* and the *vessels* connected with them. Every uriniferous tube ends in the cortical portion of the kidney in a globular dilatation called a *capsule* or *Malpighian body*, containing a *glomerulus*. The glomerulus is a small coil of

¹ Wöhler, *loc. cit.* p. 147.

vessels, produced by the branching and re-uniting of the finest twigs of the renal artery (*vas afferens*). The vessel formed by the reunion of the branches of the glomerulus (*vas efferens*), on emerging from the Malpighian body, again divides into true capillaries, which intertwine with the *tubuli uriniferi*, especially with their convoluted commencements, and finally unite with the initial branches of the renal vein.

As the blood in the glomeruli is subjected to a high pressure on account of the resistance of the second capillary system in front, a free filtration into the capsule must take place. Water and those constituents of the blood which form true solutions (salts, urea, sugar, &c.) will, therefore, pass into the *tubuli uriniferi*. Albumin, and substances which do not form true solutions, do not filter through, except under an abnormally increased pressure. The very dilute solution thus formed now comes into proximity, at the walls of the *tubuli uriniferi*, with the blood which it has just left, and which is in a concentrated state owing to the loss of water; diffusion must result (Ludwig¹), leading to a return of water into the blood, and to a consequent concentration of the urine. Besides these physical processes, other causes seem to co-operate in the formation of urine. Many circumstances lead us to suppose that the glandular cells (epithelium) especially assist; pathological degeneration of the epithelial cells, for example, interferes with secretion; and, in birds, uric acid deposits are seen to originate within the cells, the disintegration of which seems necessary before the deposits can become free; the same is observed in mammalia after the injection of sodium urate (v. Wittich, Meissner); but the most important fact is, that after the injection of certain substances into the vessels only the epithelia of the convoluted tubules are coloured by them, whilst the capsules and the straight tubules are free; the former, *i.e.* the cells of the convoluted tubulus, must therefore exert an attraction for certain substances contained in the blood; presumably they also exert such an attraction for the specific constituents of the urine; the capsules only furnish the fluid which washes these substances out of these cells. If the capsules are destroyed by caustic, the colouring matter remains in the convoluted tubules. A similar occurrence follows when, the spinal cord having been divided high up, as a result of the lowered blood pressure, the filtration in the glomeruli diminishes (Heidenhain²).

As the branches of the *vas afferens* lie at the periphery of the glomerulus, while the *vas efferens* proceeds from its centre, the flow of blood from the former into the latter is rendered easy. Any tendency to a *return* of the blood would, however, be hindered; for an increase of pressure in the branches of the *vas*

¹ Ludwig, 'Harnabsonderung,' in *Wagner's Handwörterbuch der Physiologie*.

² Heidenhain, *Archiv. f. mikr. Anat.* vol. x. 1.

efferens must force the branches of the vas afferens against the walls of the capsule and close them (Ludwig ¹).

Many authors assume that a formation of urea, uric acid, &c., from less oxidized bodies takes place within the kidneys (Hoppe-Seyler and Oppler, Hoppe-Seyler and Zalesky ²). The facts, however, upon which this theory is based, are doubted or otherwise explained by others (Meissner, ³ Voit ⁴).

The following are the points which are chiefly debated: (1.) The simple question whether the blood of the renal artery contains more urea than that of the renal vein (Picard ⁵), appears to have been recently settled in the affirmative (Gréhant ⁶); this difference disappears after ligaturing the ureters. (2.) According to some observers (Bernard ⁷ and Barreswil, Oppler, Zalesky), after extirpation of the kidneys or ligature of the renal vessels, no accumulation of urea takes place in the blood; while others (Meissner, Voit, Gréhant) maintain that such an accumulation may be detected, some even affirming that it varies in amount according to the time (Gréhant). If the former account be correct, it is still no proof of the formation of urea in the kidneys; for, after the operation, fluids containing urea and ammonia are vicariously secreted by the stomach and intestine, and are got rid of by vomiting (Bernard and Barreswil). Moreover, the animals die for the most part so quickly (of so-called 'uræmia,' whatever that may be—whether the retention in the body of some poisonous substance, or simply of water), that no considerable accumulation of urea is possible, such, *e.g.* as that which follows simple ligature of the ureters. Extirpation of one kidney does not diminish the amount of urea excreted (Rosenstein). (3.) The presence in the kidneys of characteristic bodies which do not pass into the urine (*e.g.* cystine, taurine), certainly indicates the occurrence of processes of change in the kidneys; but it does not directly prove the formation of urea or uric acid there. (4.) The accumulation of creatine, creatinine, &c., in many organs (in blood, muscles), after extirpation of the kidneys (Oppler, Zalesky), is explained by the supposition that urea is normally derived from them in the kidneys. Creatine, again, is said to undergo conversion into urea on digestion with triturated kidney substance (Ssubotin). As, however, creatine and creatinine, when administered, reappear, as a rule, in the urine, unaltered, and not as urea (Meissner, Voit), it would seem that these substances are not in general the source of the urea. In the present state of our knowledge, therefore, we must incline to the belief that urea and uric acid are separated from the blood and not formed in the kidneys.

In birds and serpents ligature of the ureters is followed by an evident accumulation of uric acid all over the body. After extirpation of the kidneys in serpents, there occur merely local deposits of uric acid (Zalesky) which lead to no decided effect. In birds, in consequence of the situation of the kidneys, they cannot be extirpated without killing the animal.

As the urinary constituents already pre-exist in the blood, the question of the source whence they are derived remains to be considered in Chapters VI. and VII.

Besides the above-mentioned circumstances affecting the secretion of urine, the following conditions influence the amount secreted in a given time, and the substances contained: 1. The quantity of urine depends (*a*) upon the intensity of the blood-pressure in the glomeruli; (*b*) upon the amount of materials of an easily

¹ Ludwig, *loc. cit.*

² Zalesky, *Ueber den Urämischen Process*, Tübingen 1865, *Centralblatt*, 1865, p. 202.

³ Meissner, *Zeitschrift. f. rat. Med.* vol. xxxi. pp. 144–223.

⁴ Voit, *Zeitschrift. f. Biologie*, vol. iv. pp. 77–162.

⁵ Picard, *Sur la présence de l'urée dans le sang*, Thèse de Strasbourg, 1856.

⁶ Gréhant, 'Thèse de physiologie pour le doctorat,' Paris 1870, *Journ. de l'Anatomie et de Physiol.* par. Robin vii. p. 318.

⁷ Bernard, *Leçons sur les propriétés des liquides de l'Organisme*, vol. ii. p. 31.

diffusible nature (water, salts, &c.) contained in the blood. This is evident, for the greater the blood-pressure the larger will be the amount filtered in a unit of time, and the greater the amount of water, salt, &c. in the blood the less will be the amount of the filtered substances which will re-diffuse into the blood vessels from the tubuli uriniferi; and, therefore, the greater will be in both cases the quantity of urine secreted. Among the circumstances which raise the blood-pressure in the glomeruli must be reckoned: 1. Rise of blood-pressure all over the body, as when the distension of the vascular system is increased (*e.g.* by a free ingestion of water, which is quickly absorbed); 2. Increased tension of the arterial system alone, produced by excessive activity of the heart; 3. Increased tension in the renal arteries, produced, for example, by ligaturing other great arteries; or simply in the glomeruli owing to a vaso-motor dilatation of the vasa afferentia; 4. Prevention of the free outflow of blood from the glomeruli through the veins (*e.g.* by the morbid contraction of the capillaries, or the ligature of the renal veins). Any very decided increase of pressure, especially when produced by the 4th of the above methods, causes, in addition, a filtration of the less diffusible portions of the blood—albumin, fibrinogen—into the urine; and an increase above a certain limit leads to the appearance in it of blood (blood corpuscles), owing to the rupture of the vessels, or, perhaps, to diapedesis. Circumstances of a nature opposite to those we have mentioned above—especially, therefore, diminished tension of the arterial system, occasioned, for example, by diminished cardiac activity (heart diseases)—must cause the amount of urine secreted to diminish. Among the substances of an easily diffusible nature referred to above, the water contained in the blood will have the greatest influence upon the amount of the urinary secretion; as a fact, the quantity secreted depends chiefly upon it, and therefore, as is explained above, upon the water ingested. The amount of each individual constituent of the urine depends (*a*) upon the amount of it previously contained in the blood, and possibly also (*b*) upon the oxidizing power of the kidneys. The following may be increased: 1. The water by ingestion (drinking), and by diminishing secretion in other ways, as by perspiring and expiring under a low temperature. 2. The salts, by an increased use of salts in food (certain salts which are formed in the body by oxidation, of course increase with the extent of oxidation). 3. The sugar, by an increased formation of sugar in the liver, or by a diminished destruction of what is formed (Chapter V.) 4. The products of the oxidation of nitrogenous bodies (considered as a whole and not as individual bodies—urea, uric acid, creatinine, &c.), by an increase in the amount of the nitrogenous foods, such as flesh, eggs, &c., which are assimilated; and also by an increased destruction of substances in the body containing nitrogen (as in excessive

nervous activity, abnormally high temperatures, fever, &c., Chapter VI.) 5. The carbonic acid, by an increase in the number of operations, especially of muscular movements (Morin), which generate carbonic acid in the body.

From what has been said above it is easy to form an idea of the circumstances which increase the quantity of urea excreted in a given time. They are (1) general increase in the urinary secretion, from whatever cause resulting; (2) free ingestion of animal food; (3) increased consumption in the body of nitrogenous material (see Chapter VII. and Chapter VIII.); and (which is doubtful) (4) increased power of oxidation on the part of the kidneys (?).

Besides the substances we have mentioned, there may be detected in the urine, after certain foreign bodies have been taken into the system, either those bodies themselves or some oxidized modification of them. The urinary secretion brings about a constant elimination of them from the body. In the case of poisonous substances, if elimination takes place as quickly as introduction into the blood, *e.g.* when absorption is taking place from the stomach, a complete immunity from danger may result. Certain easily diffusible poisons, therefore, such as curare, are harmless when taken into the stomach during a constant secretion of urine. When injected directly into the blood, or when quickly absorbed (as in subcutaneous injections), or if the activity of the kidneys is interfered with by ligature of the renal vessels (Bernard, Hermann), they act at once as poisons. As it is possible that we frequently take into the body along with food many harmful substances of this nature, their elimination by the kidneys is a further important function of those organs.

The quantity of urine excreted in twenty-four hours varies in adults (chiefly on account of the fluid ingested), between 1,000 and 2,000 grammes; the amount of urea is on the average 30 grammes, of uric acid 1 gramme, and of hippuric acid 1–2 grammes.

That the nervous system has some influence upon the secretion of the kidneys, is proved by the changes which take place in the urine referable to emotions and to nervous diseases. From the statements we possess respecting the nature of this influence, but which are not very exact (Bernard,¹ Eckhard,² Knoll,³ Ustimowitsch⁴), it would seem to be chiefly vaso-motor. Section of the nerves accompanying the renal vessels, as also of the splanchnics and of the cord, as well as lesion of a certain portion of the fourth ventricle of the brain, increase the secretion as a rule. At the same time the renal veins pulsate, the blood in them usually becoming bright carmine-red in colour, on account of the rapid flow from the arteries. Irritation of the splanchnics diminishes the secretion and the rapidity of the blood-stream through the kidneys.

Irritation of the vagus, on the other hand, is said to have an opposite effect, *viz.*, to increase the secretion and the rapidity of the blood-stream (Bernard); and therefore, like the fibres of the facial to the salivary glands (p. 131), to

¹ Bernard, *Leçons sur les prop. des liq. de l'Organisme*, vol. ii. p. 159.

² Eckhard, *Beiträge*, vol. vi. pt. 1. p. 22.

³ Knoll, *Eckhard's Beiträge*, vol. vi. pt. 1, p. 22.

⁴ Ustimowitsch, *Ludwig's Arbeiten*, 1870, p. 198.

dilate the arteries. The result of section of vaso-motor nerves is the less certain the greater the number of fibres severed. If, for example, the splanchnics or the upper part of the spinal cord be cut through, the general arterial pressure sinks to such an extent that the dilatation of the renal arteries is more than balanced. After section of the renal nerves the gland undergoes change, and the urine secreted becomes albuminous (Krimer, Brachet, Müller, and Peipers). Irritation of the skin and mucous membrane of various kinds causes the urine to become albuminous; this occurrence cannot yet be explained.

Discharge.

The urine after secretion passes out of the convoluted into the straight uriniferous tubes which unite several times at acute angles one with another, and open, at the surface of the renal papillæ, into the calyx or pelvis of the kidney. In all these situations urine is constantly found; a return of the secretion from the pelvis into the tubuli is impossible, as any increase of pressure in the former closes the openings of the latter. From the pelves of the two kidneys the urine passes through the ureters (one to each kidney) into a reservoir—the urinary bladder. The passage through the ureters may be accounted for by (1) the pressure exerted by the continually secreted urine; (2) the weight of the contained secretion (for the bladder is, in almost every position of the body, lower than the kidneys); (3) peristaltic contraction of the muscles of the ureters, which, it would seem, propels every drop of the fluid reaching the ureters by continually closing the lumen of the tube behind it.

The urine collects in the bladder (which, when empty, is collapsed in folds), until it completely fills out the walls of that organ; every further addition then causes an abnormal distension. The return of the urine into the ureters is prevented by the peculiar arrangement of their openings, which traverse the walls of the bladder very obliquely, in such a manner that pressure from within closes the channel entirely. The passage of the stored-up secretion into the urethra is controlled by a ring of elastic fibres; and, in males, by the elasticity of the prostate also. As soon as the pressure of the urine overcomes the elasticity of those structures, and a drop of urine trickles into the urethra, an impulse to micturition is felt; whereupon either the closure of the neck of the bladder is rendered firmer by the voluntary contraction of the urethral muscles (Budge), or a voluntary evacuation of the contents of the bladder is commenced. The latter is accomplished by the contraction of the muscular walls of the bladder which proceeds gradually until the lumen of the bladder is completely obliterated, and the whole of the contents are expelled. The urethra itself is next emptied by means of the muscles surrounding it (especially by the bulbo-cavernous muscle). The evacuation of the contents of the bladder is assisted by abdominal pressure (Chapter IV.)

During its stay in the bladder the urine is said by some to lose a portion of its water by absorption (Kaupp); while others, on the contrary, maintain that it receives a further addition of water from the blood, at the same time yielding up to the latter some of its urea (Treskin); and a third set of observers deny that any diffusion whatever takes place, as the bladder is unable to absorb solutions of salts so long as its epithelium is intact (Küss, Susini). Mucus from the numerous mucous glands is mixed with the urine both in the bladder and in the urethra.

The peristaltic movements of the ureter are reflex in their character, as they only occur on stimulation of the ureter by the urine forced into it, or on artificial irritation: they proceed in the direction of the bladder with a rapidity in rabbits of 20 to 30^{mm} per second (Engelmann¹). Each individual irritation of the ureter produces a wave of contraction on both sides of the point of irritation; as this may take place in portions of the ureter containing no ganglia or nerves, the wave of movement would seem to be continued by simple muscular conduction. The spontaneous movement of the ureter has been recently regarded as a case of automatic contraction of muscle (Chapter VIII.) (Engelmann).

The above theory of the closure of the bladder is disputed by some, who suppose that it is produced by a sphincter, kept constantly in a condition of contraction (tonus) by the nervous system (Heidenhain and Colberg,² Sauer, Rosenplatner, Kupressow⁶). The presence of this sphincter in man is denied by some (Barkow), but maintained by others (Heidenhain); while the existence of a constant tonus has been disputed on experimental grounds (L. Rosenthal³ and von Wittich⁴).

The nerves of the muscles of the bladder, according to some, may be traced into the cord (lower portion, Budge⁵), and even into the brain (Kilian, Valentin). They can be brought into reflex action very easily by stimulations originating in the mucous membrane of the bladder and in the bulbus urethræ. Over-distension of the bladder, therefore, causes involuntary evacuation of its contents.

In cases of degeneration of the spinal cord, retention of urine often occurs from paralysis of the detrusor, and incontinence of urine from paralysis of the sphincter.

4. CUTANEOUS SECRETIONS.

Concerning the respiratory functions of the skin, see Chapter IV.

1. Sweat.

Sweat is the secretion of the numerous tubular sweat-glands of the skin, the inner, blind extremities of which are coiled up, and lie for the most part in the corium, but sometimes in the subcutaneous layer of connective tissue, while their outer, free extremities open at the surface as the *pores* of the skin.

The sudoriparous secretion conveys out of the body the same excretory matters, generally speaking, as the urine, from which it is chiefly distinguished by the facts that it is not constantly secreted, and that it is poured out over the whole skin, and is of further use to the organism as a regulator of temperature. (The sweat-glands, therefore, bear the same morphological relationship to the

¹ Engelmann, *Pflüger's Archiv*, vol. ii. p. 243.

² Heidenhain u. Colberg, *Archiv f. Anat u. Phys.* 1854.

³ L. Rosenthal, *De tono musculorum imprimis Sphincterum*, Königsberg, 1857.

⁴ V. Wittich, *Virchow's Archiv*, vol. x. ⁵ Budge, *Virchow's Archiv*, vol. vi. p. 306.

⁶ Kupressow, *Pflüger's Archiv*, vol. v. p. 291.

kidneys as the mucous glands to the salivary glands, the glands of Brunner to the pancreas, or the sebaceous glands to the milk-glands.)

Sweat in large quantities may be obtained by supporting the body on an inclined grooved plate of metal and submitting it to a vapour bath; or by covering portions of the body with air-tight bags connected with a receiver. Sweat so obtained is almost always rendered impure by the presence of sebaceous secretion and epithelium-scales.

Sweat is apparently a colourless, clear, acid fluid of variable odour according to the part of the skin whence it was taken. The constituents of sweat are: 1. Water; 2. The usual salts; 3. Urea (and perhaps other products of the oxidation of nitrogenous bodies—Favre, for instance, mentioning an acid containing nitrogen, hydrotic acid); 4. Traces of a colouring matter (Schottin); 5. Fats; 6. Various volatile fatty acids (formic, acetic, butyric, propionic acids, &c.)

Fats predominate in the secretion of the sweat-glands of the external ear (ceruminous glands) to such an extent that it, the cerumen, resembles rather a sebaceous than a sudoriparous secretion. Sweat is easily decomposed; and decomposition may chiefly affect its fatty portions, in which case the odour of the volatile acids and the acid reaction increase; or it may chiefly affect its nitrogenous portions, when ammonia appears and the secretion takes an alkaline reaction.

The quantitative composition of sweat is about the following (in 1,000 parts): water 995.6, urea 0.04, fats 0.01, other organic matters 1.88, inorganic matters, 2.5 (Favre).

Secretion.

The secretion of sweat only takes place under certain conditions. It consists most probably in part of a process of transudation, and in part of a peculiar activity of glandular cells. The fat at least, contained in the secretion, originates in the cells; for the latter contain fat-globules, and in greater quantity the richer the secretion is in fats or fatty acids. Secretion is promoted by various circumstances: 1. By whatever raises the blood-pressure in the capillaries of the sweat-glands as, *a*, general rise of blood-pressure (*e.g.* after free ingestion of water); *b*, increase in the temperature of the body, or in the vicinity of the body, which causes dilatation of the afferent arteries (possibly by relaxing their muscles). In such circumstances the secretion of sweat is of special importance; for the evaporation of the secretion extracts heat from the body and cools it (Chapter VII.) 2. By increase in the quantity of the various constituents of sweat contained in the blood, and especially of water. Liberal ingestion of warm fluids, therefore, increases perspiration for several reasons. To what extent the above-mentioned influences must operate in order to induce ordinary secretion is unknown. The quantity secreted, of course, varies very much. Frequently no perspiration takes place for months; while, at other times, as much as 1600 grammes and more are yielded in an hour (Favre). Those portions of the skin (the fore-

head, the axillæ, the soles of the feet, and the palms of the hand, &c.) which are provided with many large sweat-glands, yield the richest supply of secretion. The value of the sweat to the whole organism is discussed in Chapters V. and VII.

From the well-known effects which the emotions exert upon the formation of a sweat it is clear that its formation must be influenced by the nervous system. Hitherto no one has been able to trace nerves to the sweat-glands. Stimulation of the nerve-trunk of a limb leads to a secretion of sweat over the skin which covers it (Goltz,¹ Kendal and Luchsinger²); this is independent of influences on vaso-motor centres, seeing that the results may be obtained on separated limbs. The secretion of sweat is, however, in all probability, like the secretion of saliva, associated with dilatation of blood vessels; the centres from the nerves of the sweat-glands and the paths which they follow appear to be the same as those of the vaso-dilator nerves; their centres may be stimulated by heat and by such a condition of the blood as would induce dyspnoea (Luchsinger³). The discharge of sweat probably is effected with the help of involuntary muscles with which the glands are provided (Hörschelmann). As is the case with the urine, substances taken into the body as food may pass into the sudoriparous secretion unchanged or oxidized. Hippuric acid is said to appear in the sweat, as well as in the urine, after ingestion of benzoic acid (Meissner). Indican also was once detected in sweat (Bizio). Cystine is present in the sweat of persons of the 'cystine-diathesis' (Gamgee).

2. Sebaceous Secretion.

The small, racemose, sebaceous glands of the skin open nearly always into hair-follicles; but the follicles are in many places so small as to appear to be simply lateral involutions of the excretory duct of the gland. The chief constituents of the sebaceous secretion are various fats, normally fluid at the temperature of the body, and cholesterin; in addition, there are found small quantities of the usual results of transudation (water, salts), and an albuminous body. It is supposed that in secretion the specific constituents (fats) arise within the gland-cells, and become free by the disintegration of the latter. Possibly the liberation of the fat-globules is due to a process of contraction similar to that which takes place in milk. The cells of the more superficial layers in the gland-cavity may be seen to contain increasing quantities of fat ('fatty degeneration'), the most superficial being completely filled. The latter then disintegrate; and hence the secretion contains fragments of cells. An influence of the nervous system upon this secretion has not been demonstrated. The secretion lubricates the hair and also the skin, giving them a shiny appearance, and preventing the entrance of fluids.

Exact experiments with this secretion, especially of a quantitative description, are wanting, as there are no means of procuring large amounts of it except

¹ Goltz, *Pflüger's Archiv*. Vol. xi. p. 52.

² Kendal u. Luchsinger, 'Zur Innervation der Gefässe.' *Pflüger's Archiv*. Vol. xiii. pp. 197-212.

³ Luchsinger, 'Fortgesetzte Versuche zur Lehre von der Innervation der Gefässe.' *Pflüger's Archiv*. Vol. xiii. pp. 891-894.

in the case of that covering the skin of new-born animals (*vernix caseosa*). The secretion of the Meibomian glands of the eyelids probably resembles the sebaceous secretion. Cerumen, on the contrary, is a secretion of sweat-glands, although there are sebaceous glands in the hair follicles of the external meatus.

The sebaceous secretion is closely allied to the following secretion—milk.

5. SECRETION OF MILK.

The milk-glands may be regarded as greatly enlarged and aggregated sebaceous glands, and the milk which they secrete as a sebaceous secretion containing a greater quantity than usual of the results of transudation.

Each gland consists of 15-24 incompletely separated racemose glands, every one of which is provided with an excretory duct, which, after dilating into a longish reservoir, opens upon the nipple. These glands are only fully developed in the female during the period of possible fertility, and they are only active from about the period of delivery until the recurrence of menstruation.

A secretion of milk takes place in new-born children, from the fourth to the eighth day; and also in rare cases in men.

Milk is an opaque white fluid, generally weakly alkaline, but frequently neutral or slightly acid (according to Soxlet the normal reaction is amphichromatic). It has a sweetish taste and a characteristic odour. It is an emulsion of very small fat-globules (milk corpuscles) in a clear fluid. Its specific gravity is 1.008-1.014.

Casein (see below) seems to belong to the list of formed elements of milk, as it does not appear in the clear filtrate obtained by filtering milk through clay by means of the air-pump (Zahn, Kehrér). It is probably contained in the fragments of cells present in the secretion (Kehrér). Many observers believe that the fat-globules possess an envelope of casein, though the running together of the milk-globules in the process of buttermaking, or even in perfectly fresh milk (Sinety) appears to be unfavourable to the surmise: the membranes seen later are of the nature of secondary precipitation membranes (haptogen-membranes).

The casein of milk is precipitated from milk which is subjected to continued diffusion, and is therefore kept in solution by the aid of a diffusible (nitrogenous) constituent (A. Schmidt).

The constituents of milk are: 1. Water, in the proportion, on an average, of about 89 per cent. 2. Salts, especially compounds of potassium, calcium, and phosphoric acid, and also of iron and manganese, the combination of the saline constituents showing a striking resemblance to that in the blood corpuscles. 3. Milk-sugar. 4. Albuminous matters, especially casein, but also a small amount of albumin; that is to say, proteids, only a small portion of which are precipitable by heat, the greater part being thrown down only on the addition of an acid. 5. Fats, viz. the glyceric ethers of palmitic, stearic, and oleic acids, and in small

quantities also of butyric, capronic, caprinic, caprylic and myristic acids. 6. Lecithin or protagon (Tolmatscheff). 7. Various 'extractives,' among others urea (Lefort). 8. Gases (CO_2 , O, N).

Human milk contains in 1,000 parts (Th. Brunner): Water 900.0, casein together with albumin (traces) 6.3, fats 17.3, milk-sugar 62.3, salts and extractives 14.1. The milk of the cow contains (Kühn): Water 885.3, casein and albumin 28.5, fats 31.2, milk-sugar 45.6, salts and extractives 9.8. Older analyses differ considerably from those here given.

Secretion.

The secretion of milk consists probably in the formation within the glandular cells of the specific constituents (milk-sugar, casein, and fat) out of the materials transuded through the walls of the blood vessels, and the liberation of those constituents by the disintegration, or some similar process, of the cell-walls. In the case of the fat, this has been directly shown to occur, the innermost layers of cells having been observed to become more and more nearly filled with fat, in the same manner as in the sebaceous secretion. These fat-laden cells then either disintegrate, or, more probably (Stricker, Schwarz), get rid of their fat-globules by contracting, like colostrum-corpuscles to be described below. The globules thus set free become emulsionized in the fluid. The milk-corpuscles, as is generally the case with fat-globules found in albuminous fluids, become coated over with a thin pellicle of some alkaline-albuminate (possibly casein). At the commencement of the period of lactation, in the so-called colostrum, or milk first secreted after delivery, certain round, unbroken, fat-laden cells (colostrum-corpuscles) present themselves. At first they are the only bodies present; but after a time they are replaced to a greater and greater extent, though never entirely, by the ordinary milk-corpuscles. It has been observed that the colostrum-corpuscles are contractile (Stricker, Schwarz), and force out their contained fat-globules; it may, therefore, be assumed that the subsequent formation of milk-corpuscles happens in like manner; and that it is only at first that the parent-cells of the milk-corpuscles themselves become free and pass into the milk. From which of the substances composing the transuded fluid the various specific constituents of milk are derived is still a matter of supposition. Casein undoubtedly originates in the albumin of the blood, as a ferment has recently been discovered in the milk-gland, which is capable of converting a mixture of albumin and an alkali into an alkali-albuminate (Dähnhardt). Milk-sugar is derived in all probability from the grape-sugar of the blood, as it is increased in quantity by the ingestion of carbo-hydrates as food; there are, however, other possible sources (Chapter VI.)

The origin of the fat is as doubtful as the method of the formation of fat generally (consult Chapter VI., where this question

is discussed); some have supposed it to be derived from alkali-albuminates such as casein (Hoppe). The process of secretion is, therefore, as yet quite uncertain; even the amount of salts contained in the milk cannot be accounted for on mere physical grounds. An influence of the nervous system, such as may and doubtless does exist, does not however seem indispensable for simple secretion, which continues after section of the cerebro-spinal nerves (in man the 4th to 6th intercostal nerves) and also of the nerves (sympathetic?) which accompany the vessels in the gland (Eckhard).

Of the special circumstances affecting the secretion, those of diet are best understood. The amount of casein and fat present during an animal diet is greater than during a vegetable diet. A liberal supply of food generally causes increase in the amount of fat, while carbo-hydrates cause increase in the amount of sugar. Fatty foods do not increase the quantity of fat. The composition varies also with the time during which active secretion has proceeded, and with other circumstances attendant upon child-bearing.

As was the case with urine, milk may contain foreign bodies (in a changed or unchanged condition) which have been previously taken into the system.

As milk contains several easily alterable constituents, and, in all probability, some ferments also, it rapidly undergoes certain changes after its secretion, which may in part be artificially induced and utilised. The ferments may be partly separated by causing milk to transude through a membrane, when they are left behind (F. Hoppe). Certain of these changes may be proved to be processes of oxidation, and are accompanied by the disappearance of oxygen and the formation of carbonic acid (Hoppe). In the first place the milk-corpuscles, which are lighter on account of the fat they contain, rise to the surface of the milk on standing, constituting the 'cream.' By means of shaking (churning), the envelopes or pellicles of the milk-corpuscles become ruptured, and in consequence the fat contained in them runs together, the fatty part of milk being thus obtained almost pure in the form of 'butter.' The remaining solution of casein, sugar, and salts constitutes 'butter-milk': as a rule, butter is manufactured by churning cream alone. Among the chemical changes occurring in milk the chief are those affecting the milk-sugar and the fats. The former gradually undergoes lactic acid fermentation, especially if the temperature be somewhat high, the milk becomes acid, and the free lactic acid precipitates the dissolved casein, causing flocculence, just like any other free acid or like the gastric juice. This coagulum, 'cheese,' includes also other of the constituents of milk, especially the milk-corpuscles. The remaining solution of sugar and salts is called 'whey.' A formation of lactic acid frequently takes place while the milk is still within the gland, the secretion having an acid reaction as soon as it is withdrawn. No oxygen is needed in the formation of lactic acid (Hoppe). On the addition of yeast, milk may, under certain circumstances (probably such as cause the conversion of the milk-sugar into lactose), undergo alcoholic fermentation; such an alcoholic preparation of milk is the 'kumiss' of the Tartars. The fats also decompose, if milk or butter be allowed to stand, into glycerin and fatty acids (caprylic, caprinic, capronic, butyric acids). Moreover, milk on standing exposed to the air, exhibits a diminution in the quantity of casein, and an increase in the amount of the substances capable of being extracted by means of alcohol and ether. This is accompanied by absorption of oxygen and liberation of carbonic acid, and is an effect (Kemmerich) of ferments of a foreign nature. In all probability this is a case of the origin

of fat by the oxidation and splitting up of albuminous bodies (Hoppe). Finally, the amount of casein increases at the expense of the albumin without the addition of air or a ferment (Kemmerich).

During the period of lactation the amount of milk secreted by both breasts in twenty-four hours amounts to about 1350 grammes.

Separation.

The withdrawal of the milk out of the flask-shaped reservoirs of the milk-ducts is brought about, as a rule, by the sucking of the young animal for whose nourishment the secretion serves, *i.e.* by atmospheric pressure. The smooth muscular fibres, which surround the whole gland, probably assist. A portion of the muscles further subserves the purpose of the erection of the nipple, which has as yet been insufficiently investigated, and which ceases to occur after section of the cerebro-spinal nerves of the mammary gland (Eckard).

6. SECRETIONS IN CONNECTION WITH THE SENSE ORGANS.

We have here to treat almost exclusively of the secretion of mucous glands, for which the same description will serve as was given in the section on Alimentary Secretions. In addition there are the cerumen of the ear (p. 156), and the secretion of the Meibomian glands (p. 158), which have been already mentioned. It only remains, therefore, to describe the secretion of tears.

Tears.

Tears are secreted by the racemose lachrymal gland, which is exactly similar in construction to the glands secreting mucus. The secretion itself may also be regarded as a very watery mucus (or saliva): it consists of a large proportion of transuded material, together with small amounts of mucin and albumin. It is clear, colourless, alkaline, and of a saline taste.

Tears contain 99 per cent. of water, 0·1 per cent. of albumin, 0·8 per cent. of salts, 0·1 per cent. of epithelium (Frerichs).

Tears are continually secreted in small quantities (Chapter X.) Their secretion is, however, considerably increased by certain kinds of psychical stimuli, or, in a reflex manner, on irritation of the nasal mucous membrane, the conjunctiva, or the retina. The impulse to secretion occasioned by irritation of the nasal mucous membrane only extends to the gland of the side stimulated (Herzenstein). The nerves, irritation of which increases secretion, and which therefore contain the secretory fibres, are the lachrymal branch of the fifth, the subcutaneous malar branch of the same

nerve, and the cervical sympathetic. Reflex stimulation proceeding from the nose may occur after section of the lachrymal nerve (Herzenstein).

As in some cases of paralysis of the facial nerve the secretion of tears is arrested, it is not unlikely that the secretory fibres for the lachrymal glands, like those for the salivary glands, spring from the facial.

The tears reach the conjunctival sac by several excretory ducts. Concerning their further application and destination, consult Chapter X.

The specific secretions of the generative organs, in which morphological structures are the essential constituents, are treated of in the Fourth Section of this book.

CHAPTER III.

RECEPTION OF MATERIAL INTO THE BLOOD. ABSORPTION.

The Materials Absorbed.

THE substances which are taken up (absorbed) into the blood are:—

1. The oxidizing body, oxygen, absorbed in the process of respiration (Chapter IV.)

2. The food or material destined for the repair of the tissues, or for the replacement of those portions of the body which are separated and cast out unchanged. Certain preparatory processes have to be passed through before absorption is possible; such processes constitute digestion.

3. The products of the chemical changes of substances which, having been absorbed by the blood and carried to the various organs of the body, have there undergone oxidation. The bodies thus formed are either gaseous (carbonic acid being the only instance) or liquid. They are, moreover, either the ultimate products of oxidation which the blood takes up simply in order to convey them to situations specially appropriated to their excretion (carbonic acid, urea, &c.); or they are compounds which are not made use of at any particular spot, but are further decomposed either in the blood itself, or after their re-secretion in some other situation. To this class belong most of the so-called 'specific constituents' of the various secretions, whether parenchymatous juices, the fluids of cavities, or free secretions, the only difference being that in the first case the constituents are reabsorbed by the blood in the place where they were secreted, while in the case of the free secretions they undergo reabsorption in other situations after they have traversed for a longer or shorter distance the channels or canals of the body.

4. Finally, a considerable amount of the materials separated from the blood in the course of secretion are reabsorbed unchanged, either elsewhere, or, if the physical conditions have in the meantime become altered, in the very place of their secretion; such substances are water, salts, albumin, called collectively 'transuded materials.'

The fourth class includes the unaltered constituents of the parenchymatous juices and fluids of cavities, as well as of pathological transudations (oedematous fluids, serous effusions). Their re-absorption into the same vessels and under the same conditions as obtained during secretion would, of course, be impossible. The conditions therefore must be changed (*e.g.* the filtration-pressure of the blood, which is continually altering, must diminish), or absorption must take place by another way (*e.g.* through the lymphatic system). The unaltered constituents of true secretions are re-absorbed elsewhere than at the place of secretion.

Methods of Absorption.

Absorption of material into the blood takes place in part directly into the blood-capillaries, and in part indirectly through the lymphatic vessels which constitute an appendage to the blood-vascular system. The capillaries of blood vessels and lymph vessels lie everywhere together. The lymphatic vessels proceeding from the alimentary apparatus, and especially from the intestine, are called lacteals.

The lymphatics and the lacteals form a simple, branched, vascular tree (comparable with that of the veins), which opens into the jugular veins at their bases by two inconsiderable trunks, viz., the thoracic duct and the right lymphatic duct. The latter receives lymph only from the vessels of the right upper portion of the body and the right half of the thorax, while the thoracic duct collects the lymph from all the remaining vessels, including the lacteals. But few accurate observations have as yet been made concerning the origin of the lymphatic vessels in the various organs. Some regard the closed network of capillaries (which are somewhat wider than blood-capillaries) as the commencement, while others suppose this network to originate in the fine, wall-less spaces of the tissues. In many compound tissues, especially in glands, the lymphatic vessels commence in fissure-like spaces between the blood vessels and the other components of the tissue, *e.g.* the glandular canals or ducts (Ludwig, Tomsa,¹ Zawarykin,² Mac-Gillavry). In the spinal cord these spaces surround the blood vessels as perivascular spaces (His³). These lymph spaces appear to be lined by epithelium. The so-called serous sacs (pleura, peritoneum, &c.), and the subcutaneous lymph-sacs of the frog, constitute similar but much larger lymphatic spaces. They are lined by epithelium and filled with lymph; and they communicate, by means of small openings ('stomata') occurring between the epithelium cells, with the lymphatic capillaries of the neighbouring tissue, *e.g.* with those of the centrum tendineum of the diaphragm (von Recklinghausen,⁴ Ludwig and Dybkowsky,⁵ Schweigger-Seidel and Dogiel,⁶ Oedmannson⁷), and especially with those of tendons and fasciæ (Genersich⁸).

¹ Ludwig u. Tomsa, *Sitzungsber. d. Wien. Akademie*. Vol. xliii. (1861) and vol. xlvi. (1862) p. 185.

² Ludwig u. Zawarykin, *Zeitschr. f. rat. Med.* Vol. xx.

³ His, *Zeitschrift für Wissenschaftliche Zoologie*, vol. xv. Translated in *Journal of Anatomy and Physiology*. Vol. i. p. 847.

⁴ V. Recklinghausen, *Die Lymphgefäße und ihre Beziehung zum Bindegewebe*; also article 'Lymphatic System,' Stricker's *Manual of Human and Comparative Histology*, Sydenham Society's translation, vol. i. p. 297.

⁵ Dybkowsky, 'Ueber Aufsaugung und Absonderung der Pleurawand.' *Ber. der k. sächs. Gesellsch. zu Leipzig*. Vol. xviii. (1866) p. 191.

⁶ Schweigger-Seidel u. Dogiel, 'Ueber die Peritonealhöhle bei Fröschen und ihren Zusammenhang mit dem Lymphgefäßsysteme.' *Ber. d. k. sächs. Gesellsch. zu Leipzig*. Vol. xviii. (1866) p. 247.

⁷ Oedmannson, *Virchow's Archiv*. Vol. xxviii. (1868) p. 361.

⁸ Genersich, 'Die Aufnahme der Lymphe durch die Sehnen und Fascien der Skelettmuskeln.' *Ber. d. k. sächs. Gesellsch. zu Leipzig*. Vol. xxii. (1870) p. 14.

The origin of the lymphatic vessels within the elementary tissues themselves must most probably be sought (Virchow¹) in the retiform canicular systems, which, according to Virchow's theory, are formed by the anastomosing cells of those tissues (connective tissue proper, bone, &c.); or which, according to von Recklinghausen, are systems of tubes bearing at their nodal points the protoplasmic masses characteristic of the tissues in which they occur. It is possible that this system of canaliculi stands, on the other hand, in direct communication with blood-capillaries, in which many observers suppose inter-epithelial openings—stomata—to occur. The same uncertainty is felt regarding the origin of the lacteals in the villi of the small intestine. The villi are small, closely-packed processes of the mucous membrane, of various shapes, but mostly conical, which give the inner surface of the small intestine the appearance of velvet. They are covered with the columnar epithelium of the intestinal mucous membrane, and possess smooth, longitudinal, muscular fibres, which produce in them a shortening and a spiral twisting on contraction (Brücke). Each contains, besides a net-work of capillary blood vessels, the disputed commencement of the lacteal, which leaves the villus as one, or sometimes several, small vessels. These lacteals originate in some way in the epithelial cells covering the villi; for all bodies which reach the chyle vessels from the intestine must first pass through them, as may be demonstrated in the case of fat-globules. Some suppose a direct union of epithelium cells, through the canicular system of the connective tissue of the villi, with the lacteal vascular system, which communicates, by means of processes, with the united bases of the epithelium cells (Heidenhain, Eimer, von Thanhoffer). Others suppose a capillary system of lacteal vessels to exist within the villi, which is, however, closed, and can only communicate by diffusion with the cells of the epithelium (E. H. Weber). A third set of observers deny the presence of such capillaries (Funke, Kölliker), and even of the central lacteal (Brücke, Basch); and think that the substances absorbed from the intestine pass through wall-less spaces, through the meshes of the tissue composing the villi, or through fissures between the blood vessels and the surrounding tissue (Basch). The same views, therefore, are held respecting the origin of lacteals as of lymphatics. The nature of the epithelium cells themselves is as much disputed as that of the origin of the lacteals. The fact that they are capable of taking up bodies from the intestine (fat-globules, pigment-granules, blood-corpuscles, &c.) has led to the supposition of openings. Each cell presents to the interior of the intestine a thickened striated end, where, if at all, the disputed openings must exist. According to some, this end consists simply of a stopper of mucus, the cells themselves being, therefore, open. Others regard the striated appearance as indication of the existence of fine perforations (Kölliker, Welcker), or of a closely-packed bundle of rods filling up the orifice, and reminding one of cilia (Funke, Brettauer and Steinach, Heidenhain, Lipsky), the interspaces of which would therefore correspond to the perforations of the preceding observers. Others, again, think that the ends are quite imperforate. A theory propounded by Letzerich differs from all those just mentioned in supposing the particles which have succeeded in reaching the lacteal vessels to have traversed certain goblet-shaped structures, situated between the epithelium cells, which anastomose below with the canicular network. These goblet-cells are thought by some (Eimer, F. E. Schultze) to be essentially secretory in function. Others regard them as simply the results of the method of treatment (Dönitz, Lipsky, Erdmann, Sachs), or as metamorphosed epithelial cells (Arnstein, Oeffinger, Heidenhain). The glandular organs connected with the lymphatic and lacteal systems of vessels will be described below. [As a result of very elaborate investigations, Dr. Herbert Watney² has come to the conclusion that the absorption of fatty matters by the villi takes place through the inter-cellular substance which connects the epithelial cells covering the villi.]

¹ Virchow, *Cellular Pathology*. ² Watney, *Philosophical Transactions*, 1876, pt. ii. p. 467

Forces concerned in Absorption.

The physical forces which are able to bring about an absorption of fluids into the blood (excluding those concerned in the absorption of gases, which are treated of in Chapter IV.), are, in the cases where it occurs through closed capillary walls, filtration and diffusion. The former in all probability only acts exceptionally, as it appears to be quite abnormal for the pressure without the vessels to exceed that of the blood within them.

Absorption into the lymphatic and lacteal vessels, the nature of the commencement of which is, as has been said, yet doubtful, is probably assisted by additional forces; such as, for instance, capillary attraction, in the case of open tubes. Filtration also may play a more prominent part here, as the pressure in the lymphatic vessels is considerably less than in the blood vessels (Noll). It is impossible to say what substances are absorbed directly into the blood, and what through the lymphatics. As, however, from the uncertainty shrouding the lymphatic and lacteal systems, we are allowed to theorise more freely with respect to the forces concerned in absorption, we may suppose that substances which do not diffuse at all, or only with great difficulty—in short the absorption of which by the blood vessels is to all appearance difficult or impossible—are taken up by the lymphatics or the lacteals. To this class of bodies belong especially solutions of albumin and fats, as well as finely divided solids (colouring matters). Water and true solutions (including peptones) are most probably taken up by both systems of vessels. The absorption of fats, also, does not appear to be confined entirely to the lymphatics, as is indicated by the greater amount of fat in the blood of the portal vein, which receives the venous blood from the intestines, as compared with that found in the blood from other vessels (Chapter V.)

An immigration of cellular structures into the blood vessels, corresponding to their emigration, has been recently observed (von Recklinghausen, Saviotti). If those cells should contain in their interior finely divided colouring matters, fats, &c., a species of direct absorption of undissolved substances would thus be accomplished.

In frogs whose hearts have been destroyed, fluids are still capable of absorption from the lymph-sacs, so long as brain and spinal cord are intact (Goltz).¹ It seems as if absorption ceases in vessels the tonus of which is completely destroyed, as soon as they have become filled; while those, the nerves of which are active, are able again and again to expel their contents, thus permitting absorption to recommence (Bernstein, Heubel, Gergens).

¹ Goltz, *Pflüger's Archiv*. Bd. v. p. 53.

Seats of Absorption.

One of the chief seats of absorption, which must now be considered separately, is the alimentary canal. The constituents of food are here partially taken up, after having undergone the changes necessary to prepare them for absorption, viz. digestion. At the same time an absorption takes place of the various alimentary secretions (mucus, saliva, gastric-juice, pancreatic-juice, bile, intestinal juice), probably in a partially altered condition, after they have performed their several functions: certain of their constituents (mucin, the specific constituents of bile) are however not absorbed, being passed out of the system in the fæces. The changes brought about in digestion, which will be more fully described below, consist in the conversion of materials, such as starch, albuminous bodies and gelatin, which are unfitted for absorption, into modifications which are easily diffusible, viz. sugar, solutions of peptones and of gelatin. A small portion also of the fat is converted into easily absorbable soap, the rest being emulsionized. Altogether, therefore, in the alimentary canal there are the following substances which undergo absorption:

1. Water derived partly from food and partly from the alimentary secretions.
2. Soluble salts, also in part derived from the insoluble salts, or the free acids and bases, taken in with the food.
3. Different kinds of sugar, all of which are derived from the food, grape sugar being, in addition, present as the result of the conversion of starch.
4. Other soluble constituents of food or of the alimentary secretions (pepsin, &c.)
5. Soaps formed from the fatty materials of the food.
6. Soluble albumin and the alkali-albuminate formed during digestion.
7. Peptones derived from the soluble and insoluble albuminous constituents of food.
8. Solutions of gelatin derived from the gelatin and gelatigenous elements of food.
9. Emulsionized fat (fat in fine globules) from food.

Of the above substances those included in the first eight classes would appear, on account of their diffusibility, to be absorbed both by blood vessels and by lacteals. All the true solutions (those mentioned in classes 1-4) are probably chiefly absorbed by the blood vessels, or, perhaps, equally by them and the lacteals; but the remaining substances are for the most part taken up by the latter. The absorption of fat, on the contrary, seems to be confined almost entirely to the lacteals.

The way in which fat reaches the lacteals is, according to the various views stated on p. 165, either through complete canals (openings in the epithelium of the villi, communicating, through the canalicular system of the connective tissue, with the central lacteal of the villus, Heidenhain); or along paths which the fat-globules find out for themselves.

In either case, the action of bile in facilitating the filtration of fat (p. 141) is most important. The forces, however, which bring about absorption are still doubtful; most probably filtration depends upon somewhat high pressure in the intestines, since the pressure in the lymphatic system is slight. Contraction of the muscles of the villi can only force the contents of the lacteals within the villi towards the larger vessels of the system, rendering no assistance whatever in the absorption of fat from the interior of the intestine. This contraction is said to be facilitated by the action of the bile (Schiff).

The absorption of fat by the lacteals is well shown by the white, milky contents of those vessels after the ingestion of fatty foods; and the favourable action of the bile in promoting it is proved by the diminution in the contents which occurs if the admixture of bile be prevented, by closure of the ductus choledochus, or the formation of a biliary fistula.

A second seat of absorption is the external skin, which, although only exceptionally active, is so often spoken of in connection with absorption that mention will be made of it here. All substances absorbed through the skin must first pass through the epidermis. The permeability of this structure appears to be usually very slight; but it may be much increased by various means (warm baths, &c.) The power of absorption possessed by the skin is proved by well-established facts.

The absorption of parenchymatous juices is still a matter of which little is known. It would appear that, apart from the absorption of these products of oxidation which are really soluble, the unaltered, albuminous constituents of transudation fluids are constantly, or under certain circumstances, taken up by the lymphatics, and the more quickly according to the rapidity with which transudation takes place, *i.e.* according as the pressure of the parenchymatous fluids in the tissue is greater. Lymph, at least, will flow from an open lymphatic vessel the more quickly according as transudation is increased either by dilatation of the arteries proceeding to the part (by section or paralysis of vaso-motor nerves), or by prevention of the escape of blood (by ligation of the veins, or compression of them by muscular contractions) (Ludwig, Schwanda). The lymphatics, therefore, may possibly have to be regarded as regulators of turgescence. The condition in which there is increased pressure of the parenchymatous fluids, and which is removed by increased activity of the absorbents, is called *œdema*. We may say that a system of drainage is continually in operation in the tissues, in which fluids are poured out of the blood vessels by transudation, percolate the surrounding cellular tissues, and finally flow away through the lymphatics. The commencements of the lymphatic vessels are, as a rule, removed as far as possible from the blood vessels (von Recklinghausen). Absorption from parenchymatous tissue appears to be

promoted by pressure such as that exerted by the contraction of neighbouring muscles (Genersich¹). Increase of arterial blood-pressure has no influence upon the formation of lymph (Paschutin²).

Destination of the absorbed Materials.

The substances absorbed directly into the blood at once form part of the plasma, from which they are in part thrown out of the body, and in part supplied to other organs.

It remains now to follow in their course to the blood the substances which are indirectly absorbed through the lacteals and lymphatics. During this course they do not remain unaltered. Their composition is materially modified after passage through certain organs, the lymphatic glands, which form part of the lymphatic and lacteal systems of vessels. They are converted into a fluid which resembles in many respects the blood into which it is about to be poured, and is, as it were, a preparatory stage of it. As these organs are not only found in the course of the larger lymphatic vessels (as ordinary lymphatic glands), but also at the very commencement of the lymphatic and lacteal systems (as so-called '*follicles*'), it is not possible to procure the original fluid as it exists immediately after absorption. The names chyle and lymph are, therefore, used to denote the modified contents of the absorbent vessels, which have already traversed glands.

The follicles, which have recently come to be regarded as the simplest form of lymphatic gland, are found in great numbers at the commencement of the lacteal and lymphatic vessels. Those connected with the former set of vessels, the lacteals, are buried in the intestinal mucous membrane, either singly ('solitary glands,' in the whole intestine), or in numbers together ('Peyer's patches,' 'agminated glands,' in the lower part of the small intestine). Those connected with the lymphatics are discovered in various parts of the body, especially in the mucous membranes of the mouth, the pharynx (the tonsils are simply collections of follicles), the stomach, and the conjunctiva, in the lungs (described for a long time as small lymphatic glands), the spleen (Malpighian bodies), and probably also in many other situations. For a description of the intimate structure of the follicles and lymphatic glands, the student must refer to Manuals of Histology; but the following account seems to embody all that is essential in their formation:—Follicles contain one cavity, and lymphatic glands many, cavities (alveoli, lymph spaces), bounded by a network of connective tissue, and traversed by a delicate reticulum of fibres and blood-capillaries; the meshes of this reticulum are closely packed with colourless, round, nucleated cells (lymph-cells). These cell-filled spaces appear to be nothing but an extended canalicular system of connective tissue, the ground-substance of which has shrunk into the fine network or reticulum of fibres. Into these spaces open either the usual connective-tissue canaliculi, or, in the case of lymphatic glands proper, the branches of the lymph-vessels proceeding to them which surround the alveoli as fissures (lymph-sinuses) lined with epithelium. From the alveoli pass out the efferent lymphatic vessels. All fluids, therefore, traversing the lymphatic system of vessels must pass through these alveoli and find their way between the cells, in which case they are brought into a relationship with the blood in the capillaries which is favourable to osmosis.

¹ Ludwig's *Arbeiten*, 1871, p. 53.

² *Ibid.* 1873, p. 51.

Lymph is a colourless or whitish-yellow fluid, which is separable under the microscope into a colourless plasma and certain nucleated contractile cells (lymph-corpuscles), fat-globules and free nuclei suspended in it. Lymph-corpuscles resemble very closely the cells contained in the alveoli of the follicles and lymphatic glands, and, undoubtedly, for the most part, originate from them. Before passing through the larger lymphatic-glands, lymph contains very few of these corpuscles, which it obtains from the follicles, or from the connective-tissue canaliculi, and probably also from the blood vessels. They completely resemble the white corpuscles of the blood. When removed from the living body, lymph coagulates like blood, only more slowly, a lymph-clot being formed while a lymph-serum is squeezed out by its contraction. It therefore contains fibrin-formers, and generates the ferment (p. 77), but not to the same extent as blood—hence the addition of blood hastens coagulation. The remaining constituents of lymph are exactly similar to those of blood, with the exception of the colouring matter, which is wanting, viz. water, salts, alkali-albuminate, protagon, fats, sugar, urea, extractives and gases (almost entirely composed of carbonic acid (Hammarsten)). It is difficult to obtain pure chyle, as it is constantly mingled with lymph in the receptaculum chyli and thoracic duct. It is distinguished from the latter fluid by the greater quantity of fat it contains during digestion, which gives to the vessels containing it a milk-white appearance. The fat forms single or united globules, larger than those of lymph. It is, moreover, taken up by the contractile lymph-corpuscles.

The motion of the lymphatic fluids towards the blood takes place under a slight pressure (Noll¹) and very slowly, chiefly on account of the considerable resistance which the lymphatic glands must offer. The forces which sustain this motion can only be guessed at: they are probably:—1. Those forces which bring about absorption of the contents into the initial branches of the system, and which, as was explained previously, are yet unknown: their effect must be to cause a gradual progression of the lymph or chyle. 2. The contraction of the various muscles surrounding the lymph-vessels, which, on account of the numerous valves existing in those vessels, forces the lymph towards the larger trunks, just as is the case in veins (p. 101). 3. The aspiration of the thorax (p. 99); for the openings of the principal trunks and the greater part of the thoracic duct also lie within the thoracic cavity.

In amphibia and certain birds (Ratitæ), the movement of the lymph is assisted by the rhythmical pulsation of lymph-hearts, of which four exist in the

¹ Ludwig u. Noll, 'Ueber den Lymphstrom in den Lymphgefäßen und die wesentlichsten anatomischen Bestandtheile der Lymphdrüsen.' *Zeitschrift f. rat. Med.* vol. 9, p. 52.

frog, two in other amphibia, and one in the ostrich. The central nervous organ connected with this rhythmical motion is said by some to be in the spinal cord, and by others in the hearts themselves. In guinea-pigs a rhythmical contraction has recently been observed (A. Heller) in the lymphatics of the mesentery. As this proceeds along those portions of the vessel between the valves with a regular progression towards the larger trunks, it must be regarded as a species of cardiac mechanism.

[In the frog the rhythmical movement of the lymph-heart seems to be dependent upon the integrity of spinal centres (Volkmann), one situated opposite the third vertebra for the anterior pair, and one opposite the sixth vertebra for the posterior pair. It is, however, affirmed (Eckhard, Schiff, Goltz, Waldeyer) that the power of regular movement may sometimes be recovered after it has been abolished by dividing the spinal nerves, supplying the hearts, or by destroying the spinal cord.

The lymph-hearts are, further, constantly inhibited from the optic lobes (Suslowa¹), this inhibition being controlled by centripetal stimuli, proceeding from skin or intestines (Goltz).²]

When the lymph has reached the blood vessels it mingles with the blood. What further use is made of it, and how it is transformed, will be described in Chap. V.

¹ Suslowa, 'Beiträge zur Physiologie der Lymphherzen. Vorläufige Mitth.' *Centralblatt*, 1867.

² Goltz, 'Reflexhemmung der Bewegung der Lymphherzen.' *Centralblatt*, 1863.

Preparation of Food for Absorption.

Digestion.

In the alimentary canal, which stretches from the mouth to the anus, the food, which has been taken into the body in a solid or liquid form, is in part directly absorbed through the walls, thus coming to mix with the juices of the tissues. The greater portion, however, has first to undergo a certain mechanical and chemical preparation. Those constituents of the food which are incapable of absorption either directly or after having passed through the various stages of digestion—the indigestible constituents—pass out of the body *per anum*, in company with certain portions of the alimentary secretions, as fæces.

I. THE CHEMICAL PROCESSES OF DIGESTION.

The secretion and properties of the alimentary juices have been described in the preceding chapter.

Water, the inorganic constituents of food, and, for the most part, the soluble organic constituents also, undergo no essential chemical alteration in the alimentary canal. If they are already dissolved, or are soluble in the secretions of the canal, they are absorbed unchanged whenever they reach the situations where absorption is possible; while, if they are in the form of free acids and bases, they are firstly combined. Certain substances upon which the alimentary juices are unable to act, and which are insoluble, also remain unchanged: to this class belong especially cellulose, and horny and elastic tissues. Such, moreover, is the fate of that portion of the soluble substances which escapes solution owing to the superabundance of the quantity ingested or to the closeness of their texture. All such materials disappear from the body *per anum*, together with certain portions of the digestive juices. The air which happens to be swallowed with the food yields up its oxygen in the alimentary canal, and receives in its place carbonic acid (Chap. IV.); hence, in the large intestine, it is chiefly nitrogen and carbonic acid which are found. The essential chemical changes of digestion chiefly concern certain insoluble, or dissolved but hardly diffusible, organic bodies, which rank among the most important elements of food; viz. carbohydrates (especially starch); albumins (albumin, fibrin, the substance of muscle, casein, &c.), both soluble and insoluble modifications; gelatin; and fats. These substances must be converted into some form which admits of absorption.

Herbivores appear to possess some arrangement for the digestion of cellulose, probably for its conversion into sugar. We are led to the supposition of a digestion of cellulose in such cases by a consideration of the large amount of it contained in vegetable foods, and the almost complete absence of it from other nutrient substances which seem nearly incapable of supporting life in those animals. In man, also, it has recently been observed that the cellulose taken into the body along with food cannot be completely recovered from the fæces (Henneberg and Stohmann,¹ Weiske). It is not known which secretion acts upon it. The cuticular substances, also, which are said to contribute to the building up of hippuric acid, must undergo digestion in the alimentary canal of herbivores, while they are indigestible by carnivores.

In the cavity of the mouth food is saturated with the alkaline fluid resulting from the mixture of saliva from the parotid, submaxillary and sublingual glands with mucus from the mouth. This saturation affords opportunity (1) for the solution of soluble, but as yet undissolved, portions of food (*e.g.* salts, sugar), and (2) for the conversion of the starch contained in the food into dextrin and grape-sugar. This conversion begins while the food is yet in the mouth and is continued in the stomach if the quantity of acid there is not sufficient to retard it.

In the stomach the following operations take place: (1) An intimate mingling of all portions of the food with one another and with the secretion of the gastric glands, viz. mucus and gastric juice. As the latter has an acid reaction, the previously alkaline mixture becomes for the most part neutralised or acidified. Many constituents of it, which were before undissolved, undergo solution in the stomach, especially such salts as are only soluble in the presence of an acid, as, for instance, the carbonates and phosphates of the alkaline earths. (2.) The conversion of starch-mucilage into sugar by means of the swallowed saliva, which continues as long as the acid reaction is not too strong. (3.) The modification of albuminous bodies, which is the chief change effected in the stomach. Fibrin, and the substance of muscle, reach the stomach almost always in an insoluble form; albumin is sometimes soluble and sometimes insoluble (*e.g.* boiled white of egg), as also is casein, which is dissolved in milk, and undissolved in cheese. Dissolved casein is, however, precipitated by the gastric juice immediately on its entrance into the stomach. As a rule, therefore, both soluble and insoluble modifications of albumin are submitted to the action of the gastric juice. Under the influence of the acid of the gastric juice undissolved albumins swell up in the stomach, and thereupon become dissolved by means of the pepsin and converted for the most part into peptones (p. 53). Soluble and insoluble albuminous substances are equally well digested (Fick). Gelatin, also, and gelatigenous tissues (connective tissue, the stroma of bone) are converted in the stomach into an ungelatinizable solu-

¹ Henneberg u. Stohmann, *Beiträge zur rat. Fütterung der Wiederkäuer*. Braunschweig, 1860.

tion. It is not certain whether the time during which food remains in the stomach is sufficient for the completion of the above-mentioned changes; but, after a liberal allowance of food has been taken, quantities of unaltered starch and undissolved albuminous substances pass into the intestine. The contents of the stomach after passing into the intestine form a pulp, for the most part acid, which is called *chyme*.

Natural digestion in the stomach has been observed, in man, through gastric fistulæ which have been the result of accident (Beaumont¹, Bidder and Schmidt²), and, in the lower animals, through fistulæ which have been made artificially. Observations have also been made upon food which had been enclosed in network bags and swallowed, and, after having remained in the stomach for a certain time, withdrawn by means of an attached string. From experiments with natural or artificial gastric juice at the temperature of the body (artificial digestion), many confirmations of the processes which go on in the stomach have been obtained.

In the intestine the acid chyme comes into contact with secretions which are entirely alkaline, viz. with bile and pancreatic juice in the duodenum, and with intestinal juice in the whole intestine. This must bring about, in the first place, a change in the reaction, which occurs earlier in those portions of the contents of the intestine touching the walls than in those which are nearer the centre. Towards the middle of the small intestine the change is complete, and the reaction is, therefore, at that point alkaline. Although the properties of each of the alimentary secretions are separately known (as was seen in the preceding chapter), little has been discovered concerning their action when mixed together in their normal condition. It has been shown that intestinal digestion, so far as it concerns the chemical changes of the contents of the intestines, and not their absorption, produces the same effect on the yet unaltered starch and undissolved albuminous and gelatinous portions of the chyme as digestion in the preceding parts of the alimentary canal. The starch, therefore, is converted into sugar, and the albuminous substances and gelatin into soluble peptones. It is also known that the fats, which have hitherto remained unaltered, are here prepared for absorption. The formation of sugar out of starch must be ascribed to the pancreatic juice, as the saliva from the mouth can no longer with certainty be shown to be present. Solution of the albuminous bodies is effected most probably by the pancreatic and intestinal juices, as the activity of the gastric juice which reaches the intestine is destroyed by the bile (p. 141.) Peptones are in part further decomposed in the intestine (p. 143), for which purpose their precipitation by the bile (p. 141) appears to be of importance, as they would be otherwise too quickly absorbed. As the result of this further decomposition, leucine and tyrosine

¹ William Beaumont, *Experiments and Observations on the Gastric Juice and the Physiology of Digestion*. Boston, 1834; Edinburgh, 1838.

² Bidder u. Schmidt, *Die Verdauungssäfte und der Stoffwechsel*. Leipzig, 1852.

are formed, and since they cannot be discovered in the fæces, are probably soon afterwards absorbed. Other products of the decomposition help to form the fæces. Finally, fats are converted into a very fine emulsion by the pancreatic juice (and probably also by bile and intestinal juice), in which form they are fitted for absorption. A portion of the fats is decomposed by the pancreatic juice into fatty acids and glycerin, which are also soluble and capable of absorption. The last named effect of pancreatic juice does not appear to occur until the contents of the intestine have assumed an alkaline reaction, *i.e.* until the lower half of the small intestine has been reached. The fatty acids resulting from the decomposition combine with alkalies to form soaps, which, in their turn, aid in the emulsification of the remaining portion of the fats (Brücke).

Besides the above decompositions, which are of the highest importance for absorption, others occur which are of no moment apparently in the promotion of that process. Thus, cane sugar, when taken into the body, is converted into grape sugar owing (according to Paschutin) to a peculiar ferment of the intestinal juice. Grape sugar, both when taken as food and when formed in the course of digestion, as well as milk sugar, are in part changed into lactic acid prior to absorption, this change taking place while they are yet in the stomach. Alcoholic and butyric acid fermentations also occur, but probably only under abnormal conditions. The gases which are yielded in these fermentations are principally carbonic acid and hydrogen, but sometimes also light carburetted hydrogen (marsh gas). The intestinal gases, therefore, consist chiefly of carbonic acid, nitrogen, and hydrogen (Chapter IV.) Salts of the organic acids, moreover, are said to become entirely or in part converted into carbonates while yet in the intestine (Magawly). The fatty acids resulting from the decomposition of fats are further split up, yielding gases and volatile products, which, together with the ill-odoured bodies formed during pancreatic digestion (p. 142), endow the otherwise almost odourless contents of the small intestine with their characteristic fæcal smell. The conjugate bile-acids undergo a hydrolytic decomposition in the small intestine, probably under the influence of the pancreatic juice; glycocine or taurine, as the case may be, and cholic acid, are the products, and the latter passes into the fæces partly in the form of its anhydrides, choloidic acid and dyslysin. There are for the most part several juices able to effect each of the chief chemical transformations which occur in the intestine; thus, digestion is not materially impaired when the co-operation of the pancreas in its operations is prevented by occluding its duct by injecting paraffin into it (Schiff).

In consequence of the chemical changes which have just been described, and of the succeeding absorption of fats and all those constituents which were soluble or had been rendered soluble, the contents of the small intestine become considerably altered in composition as they pass along the alimentary canal. Starch and the insoluble albuminous bodies which were still present at the commencement of the intestine gradually disappear, and instead of them we meet with sugar, lactic acid, peptones, leucine and tyrosine. The larger globules and masses of fat, also, which at first were mingled with the other substances, are no longer found, having formed an emulsion. The colour is yellow or yellowish brown, owing to the admixture of biliary colouring matters. Finally, all the dissolved diffusible matters and fats disappear entirely from

the mass, and the amount of water present becomes continually less and less, until at the extremity of the small intestine nothing is found but the constituents of the fæces, already possessing the characteristic odour on account of the above-mentioned decompositions and fermentations.

In the large intestine the digestive processes (*i.e.* the preparation for absorption) become less and less apparent. No new secretions are added, except the intestinal juice, which is formed here also, and absorption is restricted to water, the result being a concentration of the contents. In the human subject an absorption of albumin without its undergoing any preliminary changes has been observed to occur (Czerny u. Latschenberger¹).

(Observations on intestinal digestion are made chiefly with the aid of intestinal fistulæ occurring in man, allowing the contents of the intestine to be withdrawn and the bodies to be digested to be inserted in little muslin bags, and after sojourning in the intestine for some time, to be removed. When an intestinal fistula communicates with the large intestine, the name of 'artificial anus' is applied to it. In cases where the fistula is situated near the lower part of the alimentary canal, the changes which the injected substances have undergone on their passage to the anus may be studied (see Chap. II.)

At the end of the alimentary canal, the contents consist of fæces and intestinal gases. The former are composed of the unabsorbed residue of the food and of the intestinal secretions. As a rule the reaction of the fæces is acid, though sometimes it is neutral or alkaline; they contain water (about 75 per cent.), biliary constituents (altered bilirubin—which gives the colour to the fæces—cholic and choloidic acids, dyslysin, cholesterin), a somewhat doubtful substance called excretin ($C_{78}H_{156}SO_2$? Marcet), buccal epithelium, fats, soaps, albumin (?), indol, volatile fatty acids, salts, &c.; further, according to the quality and amount of the food, the fæces contain starch, vegetable tissues, muscular fibres, elastic fibres, &c., and, in the lower animals, hairs, bones, &c. The peculiar fæcal odour depends upon the presence of indol and volatile fatty acids.

For the quantitative relations of the fæces to the other sources of loss to the body, consult Chap. VI.]

The chemical processes of digestion have throughout the character of hydrolytic decompositions (Hermann), as a comparison of the results of digestion with the bodies submitted to that process will show. These decompositions not only appear to be favourable to absorption, inasmuch as their products are for the most part more diffusible than the original substances; but they seem to have far more important functions in 'assimilation' or the construction of the constituent parts of the body out of the nutritive materials. (Concerning this matter consult Chapters V. and VI.)

¹Virchow's Archiv, vol. lix. p. 161; Journ. of Anat. of Phys. vol. viii. p. 413.

II. THE MECHANISM OF THE DIGESTIVE APPARATUS.

The mechanical operations of the digestive apparatus comprehend: 1. The introduction of the food into the mouth, its propulsion along the alimentary canal, and the evacuation of the fæces. 2. The mechanical preparation for absorption, viz. the breaking down of solid foods and their intimate mixture with the various fluids destined to effect their chemical preparation (mastication, insalivation, &c.) These processes go on side by side.

The introduction of food is accomplished, in the case of fluid substances, by a combination of the acts of pouring into the mouth and sucking up by means of it (drinking); and in the case of solid substances by placing small pieces behind the lips and teeth, or by cutting or biting off small pieces from a larger piece by means of the incisors.

Mastication, or the breaking down of the firmer portions, begins immediately after the introduction of a piece of solid food into the mouth. It commences with a division of the food, by means of the knife-like incisor teeth, into small pieces, which are thereafter ground down between the irregular surfaces of the molar teeth at the back of the mouth. The operation of cutting is effected by an up and down movement of the lower jaw, *i.e.* by a rotation of it about a horizontal axis passing through its two articulations. The upward movement is produced by the masseter, temporal and internal pterygoid muscles, and the downward movement by the weight of the lower jaw, and by the action of the digastric, mylo-hyoid and genio-hyoid muscles, the hyoid bone being kept firm by the omo-hyoid, sterno-hyoid, thyro-hyoid, and sterno-thyroid muscles. The grinding is produced by a motion of the articular condyles of the inferior maxillary bone in their sockets in such a manner that the lower jaw is displaced with respect to the upper jaw in an anterior, posterior and lateral direction. This is accomplished in particular by the two pterygoid muscles. The morsels of food are continually pushed between the teeth by the muscles of the cheeks and lips, especially by the buccinator on the outside, and by the tongue within. The latter, moreover, has the power of crushing down softer portions of food by pressing and rubbing them against the hard palate. During digestion the food is intimately mixed with the fluids of the mouth (saliva and mucus) and forms a plastic pulp.

The nerves which control these actions are, for the proper masticatory muscles, the inferior maxillary branch of the fifth (particularly its superior division) and for the tongue and a por-

tion of the abductors of the lower jaw, the hypoglossal. The centre for the co-ordinated masticatory movements is situated in the medulla oblongata (Schröder van der Kolk).

In many animals the action of the saliva, and, in part also, the breaking down of the food, are continued in certain apparatus connected with the stomach: as, for example, in the first three stomachs of ruminants (rumen, reticulum, and psalterium), from the first two of which the imperfectly masticated food passes into the mouth before being transferred to the third; in the crop and gizzard of many birds; in the masticatory stomach of beetles; in the toothed stomach of crabs, &c.

The propulsion of solids and fluids along the alimentary canal is effected by the contraction of the circular and longitudinal muscles of its walls, which takes place in such a manner that the diminution or closure of the lumen of the canal drives the contents before it in a direction from the mouth to the anus. These propulsive contractions are called peristaltic movements; or, when occurring in the first portion of the alimentary canal from the mouth to the œsophagus—in which case they are effected by voluntary muscles—swallowing. In the act of swallowing two stages are distinguished:—1. The bolus of food situated on the anterior part of the tongue, which forms a groove with concavity upward, is pushed along towards the anterior arch of the fauces by the progressive application of the tongue to the hard palate from before backwards. 2. *a.* The anterior pillars of the fauces close-to by the contraction of the palato-glossal muscles, and, at the same time, the root of the tongue approaches the velum palati. *b.* The posterior pillars of the fauces, also, with the aid of the uvula, close-to and block up the passage between them, and the whole velum is then drawn upwards and backwards and apposed to the posterior wall of the pharynx by means of the pharyngo-palati and the levator and circumflexus palati. *c.* The hyoid bone and the larynx are approximated by the action of the thyro-hyoidei, and drawn strongly forwards and upwards by the genio-hyoidei, mylo-hyoidei, and the anterior bellies of the digastric muscles, the lower jaw, which is kept apposed to the upper by the muscles of mastication, being the fixed point. By this means the root of the tongue is bent backwards and pressed, together with the epiglottis, upon the opening of the larynx. By the actions given under *a*, a return of the food into the cavity of the mouth is prevented; by those under *b*, its passage into the pharyngeal cavity and the nose; and by those under *c*, its passage into the larynx. The morsel, therefore, propelled by the progressive contraction of the constrictors of the pharynx and the stylo- and salpingo-pharyngei, has no way left for it except into the œsophagus. While in the neighbourhood of the tonsils, which are rich in mucous glands, it becomes slimed over with mucus, and its further movement is thereby facilitated. The bolus makes its

way through the œsophagus to the stomach, partly owing to its weight, chiefly, however, aided by the peristaltic movements which in the lower two-thirds of the œsophagus are effected entirely by involuntary muscular fibres.

The propulsive movements of the alimentary canal are occasioned only by the stimulus of its contents. They appear, therefore, to be induced in a reflex manner. The movements of deglutition, for example, only occur—but then always—when a foreign body is placed behind the soft palate. They take place, therefore, whenever the posterior surface of the velum palati, the epiglottis, &c., are touched. Hence the simple act of swallowing can only be voluntarily performed, in the absence of other stimuli, by bringing some saliva behind the soft palate; and this explains why it is only possible ‘to swallow nothing’ a few times in succession, viz. only as long as there is any saliva in the mouth. The nerves which supply the muscles engaged in deglutition are: the nerves of mastication engaged in closing the jaws, the hypoglossal nerve for the tongue, the pharyngeal plexus (formed from the glosso-pharyngeal, the spinal accessory, and the sympathetic nerves) for the pharynx, and branches of the vagus for the œsophagus. The tensor palati and the mylo-hyoid muscles are supplied by the fifth nerve. The sensory fibres, which lead to reflex movements of deglutition, are contained in the palatine branches of the fifth, and in the pharyngeal branch of the vagus (Waller and Prevost); and the centre for their movements is situated in the olivary bodies in the medulla oblongata (Schröder v. d. Kolk). That the progressive contractions of the œsophagus which occur in deglutition do not depend upon the stimulation of the advancing bolus, but are the result of a central co-ordination, is evident from the fact that the wave of contraction travels over ligatures or even excised portions of œsophagus (Mosso).

Ordinarily, i.e. when the mouth is shut, the inferior maxilla and the tongue are supported by atmospheric pressure; the buccal cavity is closed in front by the lips; behind, it is hermetically shut off from the respiratory passage by the soft palate stretched over the root of the tongue, and it has a negative pressure corresponding to 2 to 4 millimetres of mercury (Mezzer, Donders).

The tongue as a whole is drawn downwards and somewhat forwards by the genio-glossal, downwards and backwards by the hyo-glossal, and upwards and backwards by the palato-glossal and stylo-glossal muscles. All these muscles, as well as the lingualis, traverse the substance of the tongue in a vertical, transverse, or longitudinal direction. By their contraction in various combinations, the tongue is able to assume the most diverse forms: thus, flattening is produced by contraction of the vertical fibres; extension and thickening by contraction of the vertical and transverse fibres; shortening by contraction of the longitudinal fibres; channelling of the upper surface by contraction of the transverse and the inner set of the vertical fibres; arching of the upper surface by contraction of the inferior transverse fibres; lateral flexion of the tip by contraction of the longitudinal fibres of one side, &c.

Even in the absence of the epiglottis, the closure of the opening into the larynx can be effected, but less securely, by the root of the tongue. The recess

or pouch between the root of the tongue and the epiglottis is so completely closed during the act of swallowing, that no portion of the fluids swallowed is able to enter it, as may be proved by the absence from it of any colouration after coloured liquids have been drunk.

Dogs can even swallow an object which is loaded with a weight of 250 to 450 grammes (Mosso).

In the stomach the larger portions of food remain for a longer time. The movements which take place there are not as yet well understood. This much may however be said: on the one hand the various parts of the contents of the viscus must be kneaded together and intermixed, and the internal portions thus made to come into contact with its walls; and, on the other, the food must be driven along the stomach and finally through the pylorus. The latter result is effected by the peristalsis, which occurs in every part of the alimentary canal. How these two varieties of movement are produced, and how they change one into the other, is almost unknown. In all probability the gastric walls are usually contracted closely upon their contents. The muscular fibres, which are present in greater numbers around the cardia and pylorus, ordinarily keep those orifices closed. The constant closure of the former has, however, been recently disputed (Giannuzzi). The closure of the pylorus is firmest at the commencement of digestion, relaxing gradually as it proceeds so as to allow the passage into the intestine, first of fluids, then of chyme-pulp, and finally even of solid material. The stomach, in course of becoming filled, rotates about a horizontal axis passing through the cardiac and pyloric openings, in such a manner that the great curvature, which usually hangs down, is turned forwards. This is not produced by any muscular action, but is a purely mechanical effect. Gases, which are swallowed with the food or are evolved in the stomach, pass out for the most part through the cardiac opening, which lies highest. The movements of the stomach are said to cease during sleep (Busch).

Concerning the nerves implicated in the movements of the stomach, all that is known is that stimulation of the vagi occasions (though not always) contractions of the stomach; and that section of the vagi materially interferes with the progress of the food out of the stomach. Some influence is even ascribed to the sympathetic. It is unknown whether the above-mentioned nerves occasion the normal movements or merely regulate them, they being initiated in local centres.

In the frog the movements of the oesophagus and stomach become very lively after section of the vagi or destruction of the cerebro-spinal organs, so that an inhibitory influence appears to be exerted by the vagi (Goltz¹).

Peristaltic movement is most marked in the small intestine. It is associated with a varying disposition of the coils of the whole

¹ Goltz, 'Studien über die Bewegungen der Speiseröhre und des Magens des Frosches.' *Pflüger's Archiv*. Vol. vi. (1872) pp. 616-642.

intestine, except the closely confined duodenum, and is constantly directed towards the anus. It gradually propels the somewhat fluid contents, as well as the enclosed gases, until they pass into the cæcum. Movement in an opposite direction is hindered by the valvular folds of the intestinal mucous membrane, and a return into the small intestine from the cæcum (the special object of which is unknown) is prevented by the ileo-cæcal valve, a fold of the intestinal wall.

In the large intestine peristalsis takes place very slowly, the contents being therefore able to remain in the sinus-like dilations of the colon for a longer time. After continuing there until, by the loss of their fluid constituents, they have assumed the characters of fæces, the contents reach the sigmoid flexure, and finally the rectum.

Evacuation of the fæces from the rectum takes place, as a rule, at intervals of twenty-four hours. Besides the peristaltic movement of the intestinal tube, the pressure of the abdominal muscles plays an important part in the operation. (Concerning this mechanism, see Chap. IV.) The sphincters of the rectum are habitually closed; their contraction, and when this ceases, their elasticity, is overcome by the force of the down-pressed fæces; the *levator ani* exerts, in virtue of its fibres which encircle the rectum, a compressing action upon the rectum, whereby, on the one hand, it can co-operate with the external sphincter, and on the other help to empty the rectum when the sphincter is relaxed (Budge). In addition, the levator ani, by stretching the pelvic fascia, furnishes the resistance necessary for the effective down-pressure of the abdominal muscles.

The nervous mechanism presiding over the peristaltic movements of the intestine is yet hidden in darkness. Seeing that these movements occur even in separated pieces of intestine, it is surmised that they depend directly upon centres situated in the intestinal wall itself, which contains ganglionic interlacements both in the mucous membrane (submucous plexus of Meissner) and in the muscular coat between the longitudinal and circular fibres (plexus myentericus of Auerbach).

Direct stimulation of the intestine occasions local contractions which occasionally progress peristaltically. The movements of the small intestine are intensified by stimulation of the vagus (not constantly), of the coeliac, mesenteric, hypogastric plexuses, of the sympathetic cord and of the spinal cord, whilst they are inhibited by excitation of the splanchnic nerves (Pflüger).

The movements of the intestine cease in warm-blooded animals if the temperature sinks below 19° C.: they become more active as the temperature increases; interruption of the flow of blood to the organ stops them (Horvath¹). As in the ureter, the transmission of peristalsis in the intestines is considered

¹ Horvath, *Centralblatt f. d. med. Wissenschaft*. 1878, p. 597.

to be due to direct muscular conduction (Engelmann and van Brakel¹). The circumstance of transmission taking place in one direction only is, however, opposed to this.

The movements of the intestine are stopped by saturating the blood with oxygen, and increased during suffocation. They are, probably for this reason, very active immediately after death. It would seem that the stimulus leading to the liberation of the intestinal movements, analogous to that causing the movements of respiration, is dependent upon the venous state of the blood in the intestinal vessels (S. Mayer and von Basch²).

The splanchnics are, at the same time, the vaso-motor nerves of the intestine; irritation of them, therefore, occasions a diminution in the amount of blood flowing to the viscera. This may possibly explain the inhibition of peristalsis, which it also produces. For the rest, if the intestinal vessels are emptied, *e.g.* by compressing the aorta, increased movement results, which ceases on again injecting the vessels with some fluid (O. Nasse³). After death, or, more exactly, at a time when the vessels are paralysed, and the capillaries contain venous blood (Mayer and von Basch), irritation of the splanchnics and irritation of the vagi both produce intestinal movements. The effects of irritation of vagi are contested, or ascribed to the contraction of the stomach, which drives the contents into the intestine (van Braam Houckgeest⁴).

The occurrence of anti-peristaltic movements of the intestine, although frequently maintained, is not yet proved. Vomiting, *i.e.* the evacuation of the contents of the stomach through the mouth, consists, not in an active contraction of the stomach, but in the compression of it by the contraction of the diaphragm and the abdominal muscles (Magendie⁵). This is shown by the fact that vomiting is still possible after the substitution of a bladder in place of the stomach (Magendie). It is, however, necessary for the success of this experiment to remove the cardia and the lowest portion of the oesophagus along with the stomach (Fantini, Schiff⁶). Vomiting, moreover, can no longer take place after poisoning by curare, which paralyses voluntary motion, while it leaves intact the nerves going to the stomach (Giannuzzi⁷). Active movements of the stomach, consisting especially of an active opening of the cardiac orifice (Schiff), may be observed in an exposed stomach during the then unsuccessful attempts at vomiting. This opening of the cardiac orifice is necessary before vomiting can occur. The central nervous organ for the act of vomiting is closely allied to the respiratory centre. Emetics prevent the occurrence of apnoea (Ochap. IV.), and strong artificial respiration prevents vomiting. It would seem, therefore, as if emetics had the power of strongly irritating the respiratory centre (Grimm⁸). This irritation also results, from an action of centripetal nerves, on injection of the emetic into the blood (Kleimann and Simonowitsch⁹). This irritation is even, when emetics are introduced into the blood, chiefly due to the agency of centripetal nerves (Kleimann and Simonowitsch); there appear, however, to exist some emetics which exert a directly central action, especially apomorphia. Very closely related in their mechanism to the act of vomiting are the phenomena of eructation (Lüttich) and of rumination (Toussaint).

Purgatives act, according to some (Moreau), by increasing the secretion of

¹ Engelmann, *Pflüger's Archiv*. Vol. iv. p. 33.

² S. Mayer u. von Basch, *Sitzungsber. d. k. Akad. der Wiss. zu Wien*. Vol. xxv. p. 580.

³ O. Nasse, *Beiträge z. Physiologie der Darmbewegung*. Leipzig, 1866.

⁴ Van Braam Houckgeest, *Pflüger's Archiv*. Vol. vi. (1873) p. 266.

⁵ Magendie, *Sur le Vomissement*. 1813.

⁶ Schiff, *Moleschott's Untersuchungen*. Bd. x. 1867, p. 353.

⁷ Giannuzzi, *Centralblatt d. med. Wissenschaft*. 1865, pp. 1 and 129.

⁸ Grimm, *Pflüger's Archiv*. Vol. iv. 208.

⁹ Hermann, Kleimann u. Simonowitsch, *Pflüger's Archiv*. Vol. v. p. 280. *Centralblatt*. 1872, p. 415.

the fluids of the intestine, and according to others (Thiry,¹ Radziejewski²) by quickening the peristaltic movements. Saline purgatives, the activity of which depends upon their endosmotic equivalent (Buchheim), and which when injected into the blood vessels produce costiveness (Aubert), act chiefly by causing the retention of water in the intestine (Buchheim).

¹ Thiry, *Sitzungsber. d. k. Akad. d. Wissensch. zu Wien.* Vol. L (1864).

² Radziejewski, *Archiv f. Anat. u. Physiologie.* 1870, Heft L.

CHAPTER IV.

GASEOUS GAINS AND LOSSES OF THE BLOOD.

Respiration.

By the term Respiration we designate those chemical processes of the animal body which are concerned in the distribution of gaseous substances, *i.e.* essentially those concerned in supplying oxygen to the constituents of the body, and in separating the gaseous product of oxidation—carbonic acid.

This process, like all others connected with the interchange of matter between the animal body and the outer world, is carried on through the agency of the blood. This fluid comes into contact, on the one hand, with the medium in which the animal lives (atmospheric air or water), abstracting from it oxygen and giving up to it carbonic acid (external respiration); on the other hand, with the animal tissues, to which it furnishes oxygen and from which it abstracts carbonic acid (internal respiration). External respiration, which is briefly denominated *Respiration*, takes place wherever the blood comes into sufficiently close contact with the respiratory medium, but chiefly in the organs specially devoted to the gaseous interchanges, and which are denominated *The Organs of Respiration*.

Atmospheric air is a mixture composed of about one-fifth (0.208) by volume of oxygen, and four-fifths (0.792) by volume of nitrogen, together with a very small and fluctuating quantity (from 0.0003 to 0.0005 by volume) of carbonic acid, and a similarly fluctuating quantity of aqueous vapour, the maximum amount of which depends upon the temperature. This mixture, at the level of the sea, is under a pressure of about 760 millimetres of mercury.

The water, which serves as the respiratory medium for many organisms, contains in solution—besides some nitrogen and carbonic acid—oxygen, which, at a temperature of 15° C. and 760 millimetres pressure, amounts, at the most, to one-twelfth (0.084) part of its volume. Corresponding to this small amount of oxygen, animals living in water require proportionally little of that element.

I. CHEMISTRY OF RESPIRATION.

External Respiration.

Respiration, properly so called, which consists in the interchange which takes place between the gases of the blood and those of atmospheric air, has its seat wherever the blood-capillaries are in intimate contact with the latter medium. This occurs especially at the external surfaces of the 'Organs of Respiration,' which will be discussed below; and, in addition, at the skin and in the alimentary canal, which always contains air, though in both these cases the process goes on with feeble intensity.

In some animals, however, *e.g.* in frogs, cutaneous respiration (perspiration) is of such importance that, after the lungs have been removed, it suffices by itself to supply the small quantity of oxygen which the animal requires.

Intestinal respiration, in consequence of the slight supply of gas, is insignificant in man; still, all the oxygen contained in the alimentary canal is consumed and replaced by carbonic acid, so that in the large intestine carbonic acid and nitrogen are the principal gases.

In many animals (*e.g.* in an air-swallowing fish, *Cobitis fossilis*), intestinal respiration appears to be important.

Outaneous respiration was formerly supposed to be of great importance, even in the case of warm-blooded animals, as its suspension, brought about by varnishing the shaven skin, causes a rapid fall of temperature and death (Bernard). According to recent researches (Rosenthal and Laschkewitsch¹), there always occurs in such cases a dilatation of vessels over the varnished area which, when it extends to the whole body, occasions such a loss of heat as to prove fatal. This paralysis of vessels, according to others, likewise occurs in internal organs, the morbid processes in which (as in the kidneys and spinal cord) play a part in inducing the symptoms (Feinberg,² Socoloff³).

Further, there are some who attribute the injurious consequences of varnishing the skin to the retention in the body of a deleterious excrementitious substance ('perspirabile retentum'); this appears to consist of a volatile nitrogenous compound. From portions of the skin which have been left uncovered by the varnish, an elimination of a volatile alkali (ammonia?) may be discovered by means of hæmatoxylon paper. Subsequently an inflammatory œdema occurs in the portions of skin which have been long kept covered with varnish, and in the serum, crystals of phosphate of magnesium and ammonium can be found (Edenhuizen); possibly the retained substance is urea, which is decomposed and generates ammonia (Lang).

External respiration consists in a passage of oxygen from the air into the blood, and of carbonic acid, aqueous vapour, and heat from the blood into the air. Respired air, therefore, leaves the

¹ Laschkewitsch, *Archiv f. Anat. u. Physiol.* 1868, p. 61.

² Feinberg, *Centralblatt f. d. med. Wissenschaft.* 1873, p. 545.

³ Socoloff, *Centralblatt.* 1872, p. 689.

body poorer in oxygen, but hotter and richer in carbonic acid and water, being almost saturated with the vapour of the latter. Corresponding to the changes in the air, the blood which leaves the lungs, in the pulmonary veins, is richer in oxygen, cooler (?), and poorer in carbonic acid and water, than the blood of the pulmonary artery. It is, consequently, of a more florid (arterial) colour. Only a small portion, however, of the loss of heat and of water which takes place is suffered by the blood in the lungs; as all parts of the respiratory passages give up heat and aqueous vapour to the inspired air.

Traces of ammonia are also excreted in the process of respiration (Thiry), but apparently in pulmonary respiration only (Schenk), so that the ammoniacal compounds which are observed when the skin has been varnished would appear to be abnormal products.

In spite of the loss of heat which the blood must undergo in the lungs, the blood of the left side of the heart, according to recent observations (Colin,¹ Jacobson,² and Bernhardt), is not cooler, but warmer than that of the right; possibly because a production of heat takes place in the lungs, owing to its combining with oxygen (Colin). This statement is denied by others (Heidenhain and Körner³). (Consult Chap. VII.)

The cause of external respiration is, in great part if not entirely, the difference between the tension of the gases in the blood and in the external atmosphere, respiration consisting in the equalization of those tensions.

The tension of the oxygen in venous blood, *i.e.* in blood which is to be subjected to the respiratory process, is smaller than the tension of the oxygen in the atmosphere, while the tension of the carbonic acid in the former is, on the other hand, greater than that in the latter. This is true not only of pure atmospheric air, but also of the air which is contained in the pulmonary alveoli, and which is much poorer in oxygen and richer in carbonic acid. In virtue of the very low tension of the oxygen of its blood, an animal placed in a confined space can consume almost the whole of the oxygen which it contains, whilst the evolution of carbonic acid is very soon stopped by an equalization of the tensions taking place (Wilh. Müller⁴).

To determine the tensions of the gases of any specimen of blood, it must be agitated with a limited volume of a gas; the tensions of the components of the latter after agitation (ascertained by determining the composition and the total pressure), are a direct measure of the tension of the gases of the blood (Ludwig⁵).

Strictly, such an experiment merely teaches the tension of the gases in the blood after agitation. Hence the result is more correct, the smaller the difference in the gaseous tension of the blood before and after agitation; *i.e.* when

¹ Colin, *Ann. des Sciences Naturelles*. Vol. vii. (1867), p. 88.

² Jacobson, *Virchow's Archiv*. Vol. li. p. 275.

³ Körner, *Beiträge zur Temperatur-Topographie des Säugethierkörpers, Inaugural Dissertation*. Breslau, 1871.

⁴ Müller, *Wiener Akad. Berichte*. Vol. xxxiii. p. 99.

⁵ Ludwig, *Zusammenstellung der Untersuchungen über Blutgase, welche aus der physiologischen Anstalt der Josefs Akademie hervorgegangen sind (Separatabdruck)*. Wien, 1865.

the quantity of blood experimented upon is relatively large, the volume of the gas used small, and when its initial tension approximates closely the gaseous tension of the blood under investigation. In order to obtain the most correct results, the blood is simultaneously but separately agitated with two volumes of gas, of which the one possesses a somewhat higher, and the other a somewhat lower tension than the gases of the blood subjected to investigation; the true gas-tension of the blood is then found by taking the mean of the tensions of the two samples of gas which have been in contact with it ('Aerotonometer' is the name given to an apparatus devised for this purpose by Pflüger and Strassburg¹).

The tension of the oxygen of the blood is, in consequence of the affinity of hæmoglobin for it, very low; but it becomes higher when the blood is heated (Worm Müller²). In the arterial blood of the dog it amounts on an average to 29·6 millimetres of mercury (*i.e.* it corresponds to the tension of the oxygen of an atmosphere which contains 3·9 per cent. of oxygen); in venous blood it amounts to 22^{mm} (2·9 per cent.) The tension of the carbonic acid is, in arterial blood, on an average 21^{mm} (2·8 per cent.), in venous blood 41^{mm} (5·4 per cent.) (Strassburg³).

The tension of the oxygen in the external atmosphere amounts on an average to 158^{mm} (20·8 per cent.), the tension of carbonic acid to 0·38^{mm} (0·05 per cent.)

The tension of the carbonic acid in the air contained in the pulmonary alveoli is so high that it may appear doubtful whether it does not exceed the tension of the carbonic acid in ordinary venous blood. Were such the case, one would have to suppose that certain influences were in operation in the lungs, capable of driving off the carbonic acid, *i.e.* of increasing the tension of the carbonic acid of the blood entering the lungs. Such influences have, indeed, been sought for partly in the absorption of oxygen, and partly in the action exerted by the lung tissue itself. To determine this point, the tension of the carbonic acid of the blood contained in the lung capillaries is directly ascertained by shaking the blood with a known quantity of the air removed from the lungs, and analysing the air before and after the process (Becher⁴). As, however, when the breath is held, the tension of the gases of the blood is very much altered, and as the air which is removed from the lungs has not equally taken part in the equalization of tension, it is a better plan to remove, for this purpose, by means of a lung-catheter, only the air from a single portion of the lung of an animal (Pflüger and Wolffberg⁵). From such experiments it

¹ Strassburg, 'Die Topographie der Gasspannungen im Thierischen Organismus.' *Pflüger's Archiv*. Vol. vi. (1872), p. 65-96.

² J. Worm Müller, *Ueber die Spannung des Sauerstoffs der Blutscheiben*, Ludwig's *Arbeiten*, 1871, p. 119.

³ Strassburg, *loc. cit.* p. 96.

⁴ Becher, *Die Kohlensäurespannung im Blute als proportionales Maass des Umsatzes der kohlenstoffhaltigen Körper und Nahrungsbestandtheile*. Zürich, 1855 (quoted by Donders and abstracted by Funke in *Schmidt's Jahrb.* 1855, vol. lxxxvi. p. 296.)

⁵ Wolffberg, 'Ueber die Spannung der Blutgase in den Lungencapillaren.' *Pflüger's Archiv*. Vol. iv. p. 415. 'Ueber die Athmung der Lunge.' *Pflüger's Archiv*. Vol. vi. (1872), p. 23.

results that the tension of the carbonic acid of the blood of the pulmonary capillaries of the dog is about equal to that of the venous blood of the heart (Wolffberg), so that external respiration is to be looked upon as consisting essentially of a simple equalization of the tensions between venous blood and the air contained in the lungs. The rapidity of gaseous diffusion in the lungs is such that, even when the respiration is free and quiet, the expired air of the dog possesses a carbonic acid tension which is nearly equal to that of venous blood (on an average 2·8 per cent. CO_2 and 16·6 per cent. of O, Wolffberg).

Nevertheless, it is possible that the simultaneous absorption of oxygen in the lungs helps to drive off the carbonic acid, though to what extent is unknown. The tension of the carbonic acid of the blood is found to be greater when the blood is agitated with a gas containing oxygen than with one containing no oxygen, or than when the blood is placed in an empty receiver (Ludwig and Holmgren¹; Wolffberg). Oxygen, therefore, increases the tension of the carbonic acid of the blood, by exerting a chemical action which serves to expel carbonic acid. Further, it is found (Ludwig and Schöffner, Sczelkow, Preyer²) that arterial blood is not only poorer than venous blood in carbonic acid which may be pumped out of it, but also in carbonic acid existing in more stable salt-like combinations. Lastly, the carbonic acid tension of serum is much lower than that of the blood as a whole, and is increased by the addition of blood, though not by merely passing oxygen through it. From these facts we should conclude that the blood corpuscles which contain oxygen exert a chemical action, by which carbonic acid, especially that existing in the serum, is liberated from stable compounds in a form capable of being pumped out of the blood.

According to J. J. Müller,³ when blood is made to flow through the blood vessels of a lung inflated with nitrogen, it gives up more carbonic acid than when it is placed in a simple chamber containing nitrogen. These researches, which ascribe some share to the lung-tissue in causing the expulsion of carbonic acid, have recently been disputed (Pflüger and Wolffberg).

The action of the blood corpuscles referred to in the previous paragraph, and which apparently can only depend upon the formation of an acid, may be imagined to take place in various manners: 1. Oxy-hæmoglobin, which has an acid reaction (Preyer), might itself possess the power of expelling CO_2 (Preyer⁴); in support of this hypothesis, amongst other facts, may be mentioned, that passing oxygen through blood furthers the crystallization of hæmoglobin, just as does diminishing the alkaline reaction of the blood by the addition of acids (Kühne).

¹ Holmgren, *Wiener Sitzungsberichte*. Vol. xlviii. (1863), p. 614.

² For references to these papers, see footnote 3, p. 64, and footnote 5, p. 186.

³ J. J. Müller, 'Ueber die Athmung in der Lunge,' *Berichte d. k. sächs. Gesellsch. der Wissenschaft zu Leipzig*. Vol. xxi. (1869), p. 149.

⁴ Preyer, *Centralblatt*. 1867, No. 18.

2. Oxygen might bring about a decomposition of hæmoglobin, leading to the formation of an acid (in certain decompositions of hæmoglobin, volatile fatty acids are generated, Hoppe-Seyler). When the gases of the blood are pumped out under such circumstances that evaporation goes on to a great extent, the strongly combined carbonic acid of blood, even, for instance, that derived from carbonates added to the fluid, is expelled (Pflüger¹); it is conceivable that in this case acids are generated by the decomposition of hæmoglobin.

3. The acid might originate in other constituents of the blood corpuscles, *e.g.* in lecithin.

4. If carbonic acid contained in the blood corpuscles were in a state of combination, say with hæmoglobin, it is possible that oxygen might expel it directly. Even in lung-tissue, whose influence in aiding the elimination of carbonic acid was suspected, an acid occurs, to which the power of expelling CO₂ was formerly ascribed, *viz.* taurine. (Oloetta; formerly this body was described under the name of pulmonic acid by Verdeil). As certain albuminous compounds (globulin) liberate carbonic acid from carbonates *in vacuo*, an attempt has been made to make use of this fact in the explanation of the respiratory process (Hoppe-Seyler and Sertoli²); this explanation does not, however, agree with the fact that oxygen has a more powerful action in expelling the carbonic acid of the blood than a vacuum.

Seeing that respiration proper consists in an equalization of the tensions of the gases existing in the blood and in the air of the pulmonary alveoli, it follows that the blood in the lungs is the richer in oxygen and the poorer in carbonic acid, the closer the air of the alveoli approaches in composition to atmospheric air. And this will depend upon the energy of the respiratory process, that is to say, upon the frequency and depth of the respiratory movements which influence in an important manner the gaseous constituents of the blood, and so indirectly exert an influence upon the gaseous interchanges of the whole organism. It is only by comparing the air inspired and expired during long periods of time that we can form a correct estimate of the gaseous exchanges of the body.

Respiration of the Tissues.

The question as to the seat of the respiration of the tissues is the same as that of the seat of the oxidation-processes which go on in the animal body. The ancient view (Lavoisier) that carbonic acid was generated in the lung itself is disposed of by the fact that the venous blood which goes to that organ contains large quantities of carbonic acid.

The increase in the quantity of carbonic acid has to be traced back to the capillaries. And it must be either within these vessels, or in the tissues outside of them, that the consumption of oxygen and the formation of carbonic acid proceed. The first of

¹ Pflüger, *Ueber die Kohlensäure des Blutes*. Bonn, 1864.

² Sertoli, 'Ueber die Bindung der Kohlensäure im Blute und ihre Ausscheidung in der Lunge,' Hoppe-Seyler's *Untersuchungen*. Heft 3 (1868), p. 350.

these two views, viz. that which places the seat of oxidation within the capillaries, is improbable, because oxidation-processes are so closely linked to the functions of organs that they must occur within them. The question would be most easily solved if we could compare the tension of the gases contained in the tissues with the tension of the gases of the blood. In general, such a comparison is impossible. The tension of carbonic acid in cavities and in fluids of the body which are surrounded on all sides by healthy tissues (as, *e.g.*, in intestinal loops and in the contents of the gall and urinary bladder) is decidedly greater even than in venous blood, pointing to the fact that the tissues give up carbonic acid to the blood; but to the place where carbonic acid originates, oxygen too must wander (Pflüger and Strassburg).

Another method of determining indirectly the tension of the gases of the tissues is to investigate the tension of the gases of the lymph (Ludwig and Hammarsten¹). In this fluid the tension of the carbonic acid is lower than in venous blood, though higher than in arterial blood. We must not from this fact conclude that carbonic acid does not originate in the tissues, seeing that the lymph experimented upon has had the opportunity, both in the connective tissue and in the lymphatic vessels, of modifying the tension of its gases by close contact with arterial blood.

One, though by itself a very insufficient, ground, for placing the seat of oxidation-processes within the vessels, appeared to be the occurrence of easily oxidizable substances (reducing substances) within the blood, especially in the blood of asphyxiated animals (A. Schmidt²). The source of the latter substances, which are contained in the blood corpuscles and not in the plasma (Afonassieff), may lie in the blood itself; lymph contains none of these substances (Hammarsten). The oxygen tension of many tissues appears to be almost equal to nothing, so that they must eagerly absorb oxygen. Muscle, for instance, contains no oxygen capable of being pumped out of it (Hermann, Chap. VIII.)

The energy of internal respiration naturally varies in the case of different organs, and in each organ it varies with the time, according to the energy of the processes of oxidation which go on within it. A comparison of the gases and of the colour of the blood of the arteries and veins of an organ supplies a measure of this energy. The blood of the renal veins is almost arterial in colour, whilst that of muscles is very dark. In the latter it appears to be more florid during activity, probably because the greater gaseous exchanges are more than compensated for by the increased flow of blood through them (Chap. VIII.)

The nature of the oxidation-processes which go on in the tissues strictly do not belong to the study of respiration; yet they must be briefly alluded to in this place.

In muscles, which are the organs in which they have been chiefly studied, oxidation does not go on directly, for the processes of absorption of oxygen and formation of carbonic acid do not occur simultaneously. (On this subject fur-

¹ Hammarsten, *Ueber die Gase der Hundelymphe*. *Ber. d. k. sächs. Gesellsch. d. Wissenschaft zu Leipzig*. Vol. xxiii. (1871) p. 617.

² A. Schmidt, *Die Athmung innerhalb des Blutes*. *Ber. d. k. sächs. Gesellsch. d. Wissenschaft zu Leipzig*. Vol. xix. (1867) pp. 99-131.

ther information will be found in Chap. VIII.) On that account the theories which connect the oxidation-processes of the body with a process of ozonizing of the oxygen, or with a formation of peroxide of hydrogen, are improbable.

Magnitude of the Gaseous Exchanges.

The magnitude of the gaseous exchanges of the body, leaving aside the variations occasioned by the movements of respiration, is chiefly dependent upon the amount of oxygen which the organism requires (for this requirement see Part II.) The more the blood is charged with carbonic acid produced in the processes of oxidation of the body, the larger the quantity of carbonic acid which is given up. Amongst the circumstances which increase either the individual or combined processes of oxidation, the following are specially to be emphasized: muscular work; a low temperature of the medium surrounding the body (which increases the production of heat in the body, so as to maintain the normal temperature, Chap. VII.); the process of digestion (which is connected with the increase of many secretions); great energy of all the vital processes (as in persons of the male sex, of strong constitution, in the prime of life, &c.)

The following circumstances exert a doubtful and disputed influence. According to the most recent researches, oxidation increases and diminishes with the temperature of the tissues; this is most clearly determined in the case of cold-blooded animals. In warm-blooded animals there appear to exist nervous arrangements which lead to an increase of the oxidation processes of the body when the skin is cooled, and to a diminution of the same processes when the skin is heated (for further details see Chap. VII.) The processes of oxidation appear to be independent of the activity of the respiratory movements (Pflüger). The food has, perhaps, an influence, in so far as a part of it appears to be directly oxidized (luxus-consumption, compare Chap. VI.); especially the ingestion of highly carbonaceous food (carbo-hydrates) appears to increase the excretion of carbonic acid.

Although in the main the absorption of oxygen and the elimination of carbonic acid proceed side by side, because nearly all oxidizable substances contain carbon, yet these two processes are very decidedly independent one of another. For, on the one hand, a formation of carbonic acid without consumption of oxygen is conceivable (the carbonic acid being one of the products of a process of decomposition); and, on the other hand, oxygen may, in some way, be stored up and not be used at once. Further information upon these relations in the case of muscles, where they are best known, will be found in Chap. VIII.

From what has been stated it follows that the numbers given below, which express the average magnitude of the gaseous exchanges, possess comparatively little value:

An adult man requires in 24 hours about 746 grammes (520 litres) of oxygen, and expires about 867 grammes (443 litres) of carbonic acid (Vierordt¹). In calculations on ventilation one estimates the hourly CO_2 -exhalation at 20 litres (a candle produces about 15, an oil lamp 60, and a gas lamp 60 litres of CO_2 in the same time).

If all the oxygen were employed in the oxidation of carbon, and all the carbonic acid formed were expired, the volume of the latter would, over considerable periods of time, be equal to the volume of oxygen, seeing that a molecule of CO_2 and a molecule of oxygen (O_2) occupy the same volume. As, however, other oxidation-processes occur (leading to the formation of H_2O , &c.), and as a portion of the carbonic acid formed is excreted in the urine, &c., it follows that the carbonic acid formed must occupy less space than the oxygen consumed, so that when an animal breathes in a confined space, a rarefaction of the air takes place. (The latter circumstance is explained also by the fact that the consumption of oxygen proceeds until the supply is exhausted, whilst the separation of carbonic acid soon diminishes and ultimately ceases.)

Under the influence of work the consumption of oxygen *per hour* may increase from 31 grammes (see above) to about five times this amount (156 grammes, Hirn²).

In man the interchange of gases through the skin, as compared with that at the lungs, is almost imperceptible. The carbonic acid excreted in 24 hours varies between 2.3 and 6.3 grammes, being on an average 3.87 grammes; its amount increases with the temperature (Aubert³).

The daily experience that exhaled air is warmer and moister than the atmosphere, and the simple experiment of breathing through a tube which dips into lime- or baryta-water, which becomes turbid in consequence, suffice to show qualitatively the differences between inspired and expired air.

In quantitative comparison, as the composition of the air inspired is known, it suffices to investigate the air expired, which for this purpose is collected in a mercurial gasometer (Allen and Pepys⁴). The air which is breathed is freed from carbonic acid and water by passing it through caustic potash and sulphuric acid.

In order to determine the total gas-exchanges which go on during long periods of time, the expired air may be allowed to pass through an apparatus in which the carbonic acid and water formed are absorbed, so that they may both be weighed. For this purpose appliances for aspirating are required, *e.g.* a vacuum (Andral and Gavarret⁵), a vessel containing water, which is allowed to run out (Scharling⁶), or an air-pump (Pettenkofer⁷). If the research has to be carried out on a large scale (as in Pettenkofer's apparatus, the air-space of which can conveniently supply a man for some time), it suffices to allow only a measured fraction of the in-going and out-going air to pass through the absorbing fluids, provided that the total volumes of the gases are continually measured (by means of gas-meters).

According to another method, respiration is carried on in a completely confined space, which is in communication only with an oxygen reservoir; the carbonic acid formed is continually being absorbed by a connected apparatus containing solution of caustic potash; in consequence of the diminution of pressure which results from the absorption, oxygen is continually being sucked from the reservoir. At the end of the experiment the amount of carbonic acid absorbed by the caustic potash is determined, as well as the nitrogen which was

¹ Vierordt, 'Physiologie des Athmens,' 1845. Article 'Respiration,' in *Wagner's Handwörterbuch*. Vol. ii. pp. 828-948.

² Hirn, *Recherches sur l'équivalent mécanique de la Chaleur*. Paris, 1858.

³ Aubert, *Pflüger's Archiv*. Vol. vi. (1872) p. 589.

⁴ Allen and Pepys, *Philosophical Transactions*. 1808 and 1809.

⁵ Andral et Gavarret, *Annales de Chim. et de Phys.* [3] 1843. Vol. viii. p. 129.

⁶ Scharling, *Annalen der Chemie u. Pharm.* Vol. xlv. p. 214.

⁷ Pettenkofer, *Annal. d. Chem. u. Pharm.* 1862. Supplementband 2.

originally present in the chamber; the oxygen which has been used is found by ascertaining the diminution which the store of this gas originally present in the chamber and the connected reservoir has undergone (Regnault and Reiset¹). Similar, though simpler, apparatuses have lately been constructed (Ludwig and Kowalewski, Ludwig and Sanders-Ezn²).

When the gaseous exchanges dependent upon the whole external respiration have to be determined, the respiratory space surrounding the whole body must be investigated. If only the respiration of the skin is to be investigated, the mouth and nose are made to communicate with the exterior by means of a tube; finally, if only the pulmonary respiration be the object of research, the respiratory chamber is in communication by an air-tight mask with the mouth and nose.

II. THE MECHANISM OF RESPIRATION.

In the lowest organisms, the bodies of which are but small, the mere bathing of the body in the medium to be breathed (water) is sufficient to keep up the interchange of gases by diffusion; more highly developed animals of larger size require a larger surface for the proper interchange between the juices of the body on the one hand and the medium on the other. In animals in which the blood-vascular system is either in a rudimentary state or altogether wanting, the medium must be introduced into and distributed over all parts of the body in order to be everywhere brought into contact with the juices; but where the blood-vascular system is fully developed, the mass of the blood can be passed into an organ of large surface, where it can meet the medium to be breathed, and where, thus, over large surfaces the blood can enter with it into the process of diffusion.

The arrangement in the first class consists of a system of branched tubes, as in the *water-vascular system* of echinodermata and scolecida, and the *tracheal system* of arthropoda: while in the latter class we have an *eversion* of the body surface if water is breathed, as in the *gills* of mollusca, fishes, and the larvæ of batrachia; or an *involution* if air is breathed, as in the *lungs* of amphibia, birds, mammals, and man. As a separate respiratory medium for the foetus of mammals and of man, we have the oxygenated maternal blood, which meets the blood of the foetus in the placenta (foetalis and uterina), where through the walls of the capillaries the gaseous exchange takes place (Chap. XII.)

The human respiratory organs,³ the lungs, represent two elastic bags, containing a branched system of tubes with terminal vesicles (alveoli), and the surface in each alveolus being further extended by the presence of prominent ridges in its walls. The cavity of each lung communicates by means of the trachea, larynx, pharynx, and the nasal or oral cavity, with the external air.

The lungs left to themselves contain no air: they are *atalectic*, like the lungs of the foetus before it has 'breathed,' *i.e.* the

¹ Regnault et Reiset, 'Recherches chimiques de la respiration des animaux de diverses espèces.' *Ann. de Chimie et de Physique*. 3me série, vol. xxvi. (1849) p. 299. In these experiments an increase of the nitrogen in the respiratory chamber was observed, which may be explained either by supposing that an elimination of nitrogen occurred in the process of respiration, or that there was a slight leaking of air into the apparatus. Occasionally the former phenomenon appears to occur; occasionally, on the other hand, there would appear to be a respiratory absorption of N (Ludwig and Scheremetjewski). This subject requires, however, further investigation (compare Chap. VI.)

² Sanders-Ezn, 'Der respiratorische Gasaustausch bei grossen Temperaturänderungen.' *Ber. d. k. sächs. Gesellsch. d. Wissenschaft zu Leipzig*. Vol. xix. 1867, pp. 58-99.

³ The cutaneous and intestinal respiration, not possessing a separate mechanism, are not considered here; their importance in man is but small.

walls of its tubes and of its alveoli lie in apposition by virtue of their elasticity. In the human body, however, the lungs are so fitted into an unyielding reservoir (the thorax) that no air can pass between their external surface and the internal surface of this reservoir (more accurately, between the pleural surface of the lungs and the lining of the thorax). The pressure of the atmospheric air entering the lungs must necessarily therefore expand them against their own elasticity to more than their normal volume; they closely apply themselves to the thoracic walls, and are therefore during life always found filled with air. Should, however, through any opening, air pass into the space between the lungs and the thoracic walls, then the lungs by virtue of their elasticity collapse to their natural (atalectic) volume (Pneumothorax).

Not only the lungs, but the heart and vessels also, contribute towards the filling up of the thoracic cavity. The pressure of the air acts upon the inner surface of all these organs; it acts directly (through the trachea) on the lungs; it acts indirectly on the heart, for the whole body, and therefore all the vessels situated outside the thorax, and communicating with the interior of the heart, are under atmospheric pressure. The same pressure then tending to enlarge all the hollow organs within the thorax, these organs will expand according to their degree of expansibility, and hence the most expansible organs, the lungs, will contribute most towards the filling up of the thorax (they will be dilated the most beyond their original volume), the thick-walled ventricles the least, while the thin-walled auricles and the venous trunks will be perceptibly dilated. The atmospheric pressure acting equally upon the external surface of the thoracic walls, their more yielding parts will likewise contribute towards the filling up, or rather the diminution of the thorax: hence the diaphragm and the intercostal spaces will arch in towards the thorax.

The following model illustrates these relations. A bottle provided with a stopcock, *o*, contains two elastic bags, represented in fig. 14 in their natural configuration; the one, hourglass-shaped, with a thin-walled and thick-walled division, *v* and *κ*, is filled with a fluid and communicates with an open vessel containing water; this double bag represents the heart (*v* = auricle, *κ* = ventricle), the other bag, *l*, filled with air and communicating through *t* (= trachea) with the atmosphere, represents the lung. The membrane *i* represents the soft parts of an intercostal space. Fig. 15 shows the apparatus after the air has been exhausted, through *o*, from the bottle. Both bags, on the inner walls of which the atmospheric pressure acts (indirectly on *v κ*), are seen expanded, filling up completely the interior of the bottle; *l* is most expanded, *v* much less, and *κ* the least; *i* is also seen to be somewhat vaulted in. If now through *o* air is again allowed to enter, we get again the same condition of things as in fig. 14, which corresponds to the condition of pneumothorax.

Each of the two bags in fig. 14 tends to contract at the expense of the other, i.e. to extend the other. The figure represents the state of equilibrium. Hence in the usual representation of the relations in the thorax, lungs expanded above their normal volume are made to exercise a pull ('negative pressure') on the heart and the soft parts of the thoracic walls (represented by arrows in fig. 15), but we have also to consider that the heart, &c., acts in the same way on the lungs.

We are able to measure manometrically the elastic force with which the lung, when expanded to the size it has in the passive thorax, tends to contract (or in other words, its negative pressure when the thorax is at rest), by fixing a manometer air-tight into the divided trachea of a dead body and then opening the thorax; this elastic force is about 6 mm. of mercury (Donders). The elastic

force of the expanded lung may be further assisted by the non-striped muscles surrounding the bronchial tubes, for by their contraction the bronchial tubes would be narrowed, and therefore the negative pressure in the thorax increased, whereby a greater expansion of the other organs would be effected. We know,

FIG. 14.

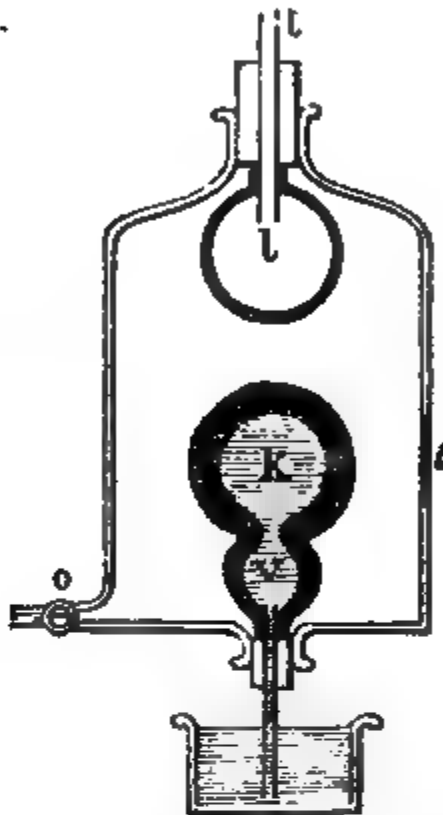
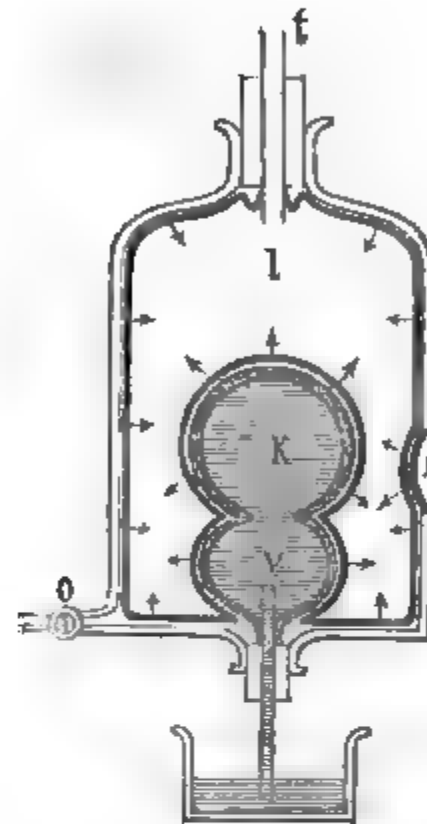


FIG. 15.



however, nothing definite either about the time and mode of this contraction or about the innervation of the muscles. Irritation of the pneumogastric diminishes slightly the volume of the lung, when the latter is cut out and ligatured (Schiff).

The Respiratory Movements.

The air in the pulmonary alveoli comes into contact with the blood of the capillaries, which enmesh them; and in this contact the gaseous interchange is effected. As already explained, the result is a loss, on the part of the alveolar air, of oxygen and a gain of carbonic acid, which very speedily unfit it for further use. This might be remedied by diffusive exchanges—extending from layer to layer—of air within the lungs, and reaching at last the atmosphere. But such a series of exchanges would be altogether too slow for the requirements of the blood; therefore mechanical means are employed to produce a frequent ventilation of the recesses of the lung, these means being periodic contractions and expansions of the whole organ. The thorax, in which the lungs are placed, is alternately enlarged and diminished in the acts of 'Inspiration' and 'Expiration,' and the lungs of necessity follow its changes.

The enlargement of the thorax, or *Inspiration*, is always the result of muscular action. The ordinary inspiratory muscles, those concerned in ordinary inspirations, are: the diaphragm, the

scaleni and the intercostal muscles—especially the external. In deeper inspirations, whether intentional or forced, owing to some obstruction, additional or ‘accessory’ inspiratory muscles come into play. These are, the serrati postici and the levatores costarum as a first reserve; and the sternocleido-mastoids, the pectorals, the serrati antici, and many more, in cases of the greatest respiratory distress.

Increase of thoracic capacity is chiefly brought about by the diaphragm, which, especially in its muscular parts, becomes flattened on contracting. Moreover, its borders, which are closely applied to the walls of the thorax during rest, are withdrawn therefrom in the act of inspiration. The remaining muscles act, in the majority of cases, upon the ribs; they have, in general, a course from above downward and forward; they are fixed at their attachments by means of the spinal column, or—as in the cases of the pectorals and the serrati antici—of immovable portions of the upper extremity, and hence come to draw the ribs outwards and upwards, whereby the thorax is enlarged.

Each rib is, in virtue of its articulation to the bodies and transverse process of the vertebræ, able to rotate about a horizontal axis. The axes of rotation of each pair of ribs converge forward so as to include between them angles which diminish from above downward, being 125° in the highest rib and 88° in the lowest (Volkmann). Every elevation of a pair of corresponding ribs, i.e. every upward rotation of them about the above-named axes, brings the inclined plane of that pair of ribs nearer the horizontal, and so enlarges the transverse section of the thorax. This rotation of the ribs about their axes is, however, confined somewhat narrowly by the pliant but elastic cartilage which attaches them to the sternum. Hence, at every elevation of the ribs there follows, beside a raising of the sternum, a slight torsion of the costal cartilages about their long axes. As a further consequence of the different degrees of convergence of the axes of rotation in the successive pairs of ribs, may be mentioned the following. The upper ribs, whose axes incline to run parallel to the transverse diameter of the thorax, will, on being elevated, enlarge the thorax mainly in an antero-posterior direction; while the lower ribs, whose axes incline to coincide with each other and with the antero-posterior diameter of the thorax, will enlarge the thorax mainly from side to side.

A consideration of what has now been said about the disposition of the movable parts will render clear the action of the rib-lifting muscles. How far the intercostal muscles are to be regarded as elevators of the ribs may be seen from the following diagram (Hamberger). Let RR' and rr' be the *posterior* portions of two neighbouring ribs having the downward and forward inclination of the position of rest; and RR'' , rr'' , the same ribs in the position of inspiration. Further, let ab represent a fibre of the external intercostals, and cd a fibre of the internal intercostals. It is at a glance obvious that the fibre ab is shorter in the raised position of the ribs (as $a'b'$), while the fibre cd is shorter in the lowered position.¹ Hence contraction of ab must raise both ribs, while

¹ If the angle $rRb = x$,
then

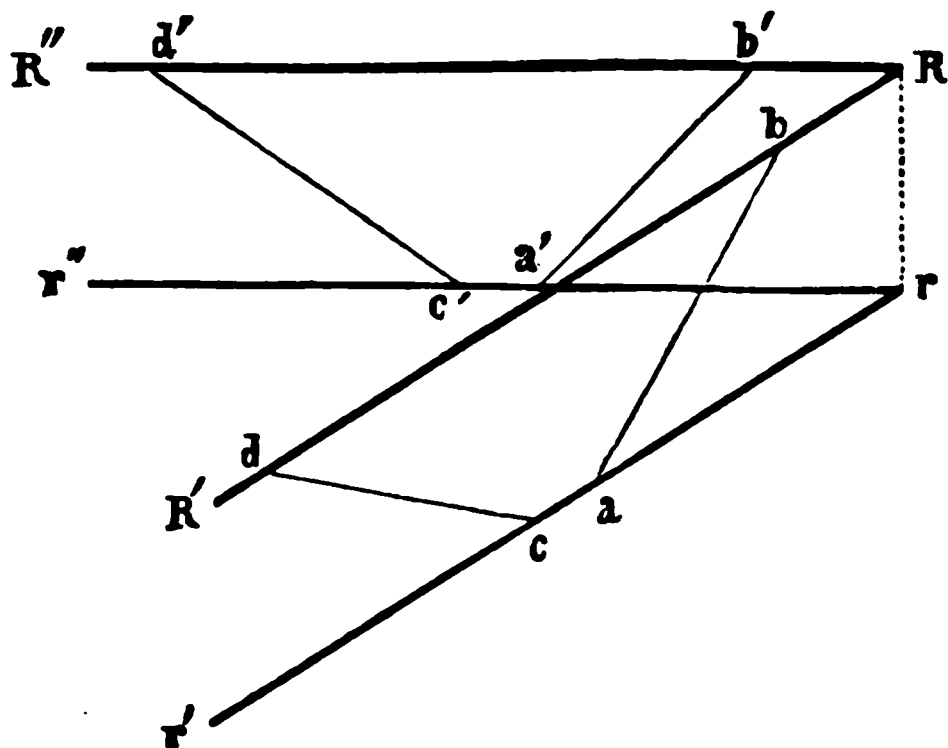
$$ab^2 = Rr^2 + (ra - Rb)^2 + 2Rr(ra - Rb)\cos x$$

$$cd^2 = Rr^2 + (Rd - rc)^2 - 2Rr(Rd - rc)\cos x;$$

hence ab will be larger the *smaller* the angle x , and cd will be larger the *larger* the angle x , for the cosine increases as the angle diminishes.

contraction of *cd* must depress them both. On the other hand, the fibres of the same muscles situated in the *anterior* portions of the intercostal spaces, between the costal angle and the sternum, have exactly the opposite effects on contraction. In this situation the internal intercostals are inspiratory muscles, while the external are expiratory. Hence, the external intercostals that are fixed to bones, and the internal intercostals that are fixed to cartilages, are all inspiratory. But since the external intercostals are, for the most part, osseous, while the internal intercostals have their most important attachments to cartilage, both sets of muscles may be roughly spoken of as inspiratory in function.

FIG. 16.



It must, however, be stated that the action of these muscles is not yet experimentally established.

While the elevators of the ribs enlarge the area of cross-section of the thorax, the contracting diaphragm increases its long axis. According as the former or the latter mode of enlargement predominates, it is usual to distinguish two types of breathing, the *costal* and the *abdominal*. The latter term is suggested by the marked protrusion of the abdominal wall, which follows the descent of the diaphragm, and the consequent pressure on the contents of the abdomen during respiration of the abdominal type. Costal movements chiefly mark the respiration of women, abdominal movements that of men.

The alternate action of *Expiration*, or the diminution of the capacity of the thorax, is, as a rule, effected by the weight and elasticity of the disturbed parts on the removal of the disturbing, or inspiratory, force; the parts returning to the original position of equilibrium. Gravity determines the fall of the ribs; the elasticity of the lungs draws the diaphragm upward and the thoracic walls inward; and the elasticity of the twisted costal cartilages forces the ribs back again to their original places. But in forced or obstructed expiration muscular action is called into play, the expiratory muscles having in general a direction from behind forward and upward. The chief expiratory muscles are the abdominal muscles, which by their contraction compress the abdominal viscera and force upward the diaphragm. They, moreover, drag the ribs downward; as do also the quadratus lumborum and the serratus posticus inferior on each side. The ribs are, further, depressed by

those fibres of the internal intercostals that stretch between bones, as has already been explained. How depression of the ribs lessens the volume of the thorax will be at once evident on reflection.

The passages leading into the lungs also take part, at certain times, in the movement of respiration. Thus the *rima glottidis* widens during inspiration; and, during forced inspiration, the nostrils also are dilated by the levator muscles of the nasal alæ; both acts facilitating the entrance of air into the lungs.

Since the lungs, as before stated, must needs follow the movements of the thoracic walls, every inspiration brings about an enlargement of the lungs in the transverse and longitudinal diameter, and—since the diaphragm withdraws from contact with the thoracic walls—in parietal area also. The last mode of enlargement is evidently associated with a down-drawing of the whole lung along the walls of the thorax, which would of itself, even without any simultaneous increase in the cross-section of the thorax, lead to an enlargement of the cross-section of the lungs; for, since the thorax is conical in form, every cross-section of the lung would, in being drawn down, come to occupy a lower and therefore larger cross-section of the thorax. This sinking of the lungs within the thorax, further, leads to a downward movement of the trachea and larynx in inspiration, an effect easy to be observed in the living subject.

The enlargement of the lung on inspiration, which affects all the recesses of the lung, but chiefly the most yielding of them—viz. the alveoli—leads to an increase in the gaseous contents of the lung. This increase, in quiet breathing, comes to about $\frac{1}{8}$ th of the whole contents; but a far larger increase is possible during deep inspirations. A measure of the limits of this increase is to be found in what is known as the 'vital capacity' of the lungs. This term is applied to the difference between the amount of air contained in the lungs when as full as possible, and the amount contained in them when as empty as possible; or, in other words, the amount of air which may be expelled from the lung during the deepest possible expiration after the deepest possible inspiration (Hutchinson). This amount stands in a pretty constant relationship to the size of the body, but varies somewhat according to occupation and sex; being larger in proportion in men (Arnold). In adult men it is equal to about 3770 cubic centimetres.

In order to measure the vital capacity, use is made of the 'spirometer' (Hutchinson), which is a bell gasometer with equipoised cylindrical bell, into which air may be driven through a flexible tube. A deep inspiration is taken by the person to be tested, and as much air as possible expired down the tube into the gasometer, and the volume of expired air read off according to the height the bell has been raised. Gas-meters also may be used for this purpose.

In addition to 'vital capacity,' there are other terms and measurements which must be here mentioned. In the first place, there is the term 'residual air' (Hutchinson), or the amount of air still left in the lungs after the deepest expiration. This may be determined by breathing from a receiver containing hydrogen gas until no further change in the composition of the gases of the

receiver follows; that is to say, until the hydrogen has become intimately mingled with the air in the lungs. If now, as deep an expiration as possible be given, we shall be able to determine the amount of gases still left in the lungs, knowing the composition of the expired mixture and the amount of hydrogen which is missing (H. Davy, Gréhant¹). In the next place, there is the amount of air contained in the lungs after an ordinary expiration, which is determined as in the case of 'residual air.' The difference between this amount and the 'residual air,' or the amount of air which may still be expired after an ordinary expiration, is known as 'reserve air.' Similarly, the difference in amount of air in the lungs after an ordinary inspiration and after a forced inspiration is called 'complemental air.' The difference between the amounts of air in the lungs after ordinary inspiration and ordinary expiration is called 'tidal air.' If the 'residual air' be called a , the 'reserve air' b , the 'tidal air' c , and the 'complemental air' d , then $b + c + d$ equals the 'vital capacity.'

Respecting the *chemical* renewal of the gases in the lungs, it has been discovered, by means of the respiration of hydrogen gas (Gréhant), that a portion $a.c$ of the amount of air c taken into the lungs between any two expirations, remains within the lungs, becoming equally mixed with the gases already there.

(If $c = 500$, then $a.c = 330$.) In ordinary respirations, therefore, $\frac{a.c}{a+b+c}$ equals the volume of new air—new, chemically speaking—which the unit-volume of the lung-space receives at each inspiration. This amount is called the 'coefficient of ventilation:' thus, if $c = 500$, $a+b+c = 2930$, then $\frac{330}{2930} = 0.113$.

It has, moreover, been found, by taking a single inspiration of hydrogen gas and then breathing air, that an amount of gas inspired equal to 500 cubic centimetres does not, in ordinary respiration, entirely disappear from the lungs until the sixth to the tenth respiration has been taken (Gréhant).

To determine the movements of the thorax a 'chest-measurer' is used (Sibson), which is an instrument for registering the changes in the horizontal antero-posterior diameter of the chest. The instrument is so applied that the anterior chest-wall pushes before it a rod which moves an index; the axis of the indicator is fixed by means of a frame to a board upon which the body rests in a horizontal position. Similar apparatuses measure at the same time the excursions of the chest-wall in several diameters (Ransome²); and further modifications of the apparatus have been devised to give graphic records, and are called 'Stethographs' (Riegel). The 'Pneumograph' or 'Atmograph' of Marey is a girdle, in the course of which an elastic cylinder is interposed, the capacity of which is enlarged by the movement of inspiration, and the consequent changes of pressure in the interior of which are graphically recorded by means of tambours and writing-levers. By this means the variations in the circumferential measurements of the chest are taken; but in the same manner, viz. by making use of the compression of air in drums, &c., the diametric changes may also be recorded (Fick). In the lower animals the movements of the diaphragm may be also determined; either by means of a needle piercing the body-walls and stuck into the diaphragm (Snellen), or by means of a lever introduced into the abdominal cavity and placed in contact with the abdominal aspect of the diaphragm. In the latter case the lever may be made to record its movements as curves upon a strip of paper passed in front of it, and the instrument is then called a 'Phrenograph' (Rosenthal).

Since the thorax becomes enlarged during inspiration, all the hollow viscera contained within its walls must tend to expand; and hence the 'negative pressure' (p. 194) under which the heart and thoracic vessels exist is increased, and the aspiration which they normally exert on their contents intensified (p. 99). On the other hand, the act of expiration, which in ordinary cases

¹ Gréhant, *Journal de l'Anatomie*, vol. i. p. 523.

² Ransome, *On Stethometry*. London, 1876.

merely removes the inspiratory increase of negative pressure, may, if forced, completely annul it or even convert it into a positive pressure. Thus the pressure becomes positive when, during active expiratory efforts, the expulsion of air from the lungs is hindered by closure of the *rima glottidis*. The aspiration of the thorax is by some considered to quicken the current of the blood through the lungs (Haller, Quincke and Pfeiffer), but by others to slow it (Poiseuille, J. J. Müller). Increased pressure in the air passages slows the pulmonary circulation (Quincke and Pfeiffer). The pulmonary vessels are very extensible and have but slight tonus, so that closure of large arterial trunks of the pulmonary system hardly affects the greater circulation (Lichtheim). Concerning the vaso-motor mechanism of the lungs consult p. 113.

The pressure of the air in the introductory air-passages, which is like that of the atmosphere when the subject is not breathing, undergoes slight variations during the respiratory cycle, owing to the constricted orifices of nostrils and larynx. These are: a negative pressure, equal to about -1 mm. in inspiration, and a positive pressure, equal to from $1-3$ mm. in expiration. This may be demonstrated, in the case of animals, by connecting a manometer laterally with the trachea, and, in the case of man, by fixing a manometer into one nostril and breathing through the other while the mouth is kept closed. The manometer under these circumstances also shows variations of pressure of cardiac origin, since the amount of blood in the thorax varies with the phases of the cardiac cycle (Ceradini, Landois).]

The friction against the walls of the larynx and the system of tubes through which the current of air passes during each inspiration, gives rise to *murmurs* audible by the ear applied to the chest-wall. In the unyielding parts (larynx, trachea, and larger bronchi) this murmur has a more whiffling, breezy character ($= h$ or ch , '*bronchial murmur*'); in the smallest bronchi, where the air has to force its way through narrow channels, it is more of a sipping, hissing, or whizzing nature ($= v$ or f , '*vesicular murmur*'). In the superficial respiration (of grown-up men) the character of the murmur becomes indeterminate; in like manner regular expiration produces an indistinct weak murmur. [Many consider the '*vesicular murmur*' also to arise in the large air-passages, i.e. they regard it as a '*bronchial murmur*' modified by passing through a parenchyma filled with air.]

Rhythm and Innervation of the Respiratory Movements.

The movements of inspiration and expiration can be produced at will. Ordinarily, however, they are involuntary, and have a certain rhythm and a certain intensity or depth.

We are able at will to vary both, in any manner we like; but total cessation is only possible for a very brief period of time. The medium frequency of respiration in an adult is 18 per minute.

The respiratory movements are comparatively frequent in the very young and the very old, in the female, at high temperatures, during muscular effort, during digestion; they are increased under the influence of emotions, and after a temporary suppression of respiration, these agencies being the same as cause an increased frequency of pulse. In general one respiration corresponds to four heart's contractions. The influence of the passions affects not only the frequency but also the depth and the form of the respiratory movements; the latter producing thereby sometimes characteristic sounds or murmurs in the tubes which conduct the air to the lungs. To this category of characteristic sounds belong: *sobbing*, when the inspirations succeed each other quickly; *sighing*, when a deep inspiration is followed by a forced expiration; *yawning*, when there is slow and prolonged inspiration while the mouth is kept spasmodically opened; *laughing*, where there is a jerking, interrupted expiration; &c.

The impulse to the involuntary rhythmical respiratory movements proceeds from a circumscribed spot in the medulla oblongata, which is situated at the place of origin of the pneumogastric and spinal accessory nerves (Chap. XI.): the destruction of this spot suppresses at once all respiration, and is therefore fatal ('*Nœud vital*,' Flourens). From this spot the diaphragm is acted upon through the phrenic nerves, and the other inspiratory muscles through the external thoracic nerves; expiration also, as far as muscular forces are concerned in it, is under its influence. The rhythm of the excitations of the respiratory centre is influenced by certain fibres which run in the course of the pneumogastric, and which are in a constant state of irritation. There are two kinds of these fibres: the one kind are accelerating; the other, which the pneumogastric receives from the Ramus laryngeus superior (Rosenthal¹), or according to other authors (Pflüger and Burkart,² Hering and Breuer³) from other nerves, particularly the Ramus laryngeus inferior, are retarding, regulating or inhibitory. Ordinarily the excitation of the former (the accelerating) fibres predominates; for after division of one or both vagi (in the neck) the respiratory rhythm becomes slower (Traube⁴): on artificial irritation also of the central end of the divided vagi, the excitation of accelerating fibres usually overbalances the other (the inhibitory), respiration in consequence becoming quicker: if the irritation is stronger still, it becomes tetanic, *i.e.*, the diaphragm remains in a state of contraction—inspiration (Traube). At times, however, we have the opposite effect on strong irritation, namely, the arrest of the diaphragm in a state of relaxation—expiration: this is particularly the case on the fatigue of the nerves, the result being due to the fact that the inhibitory fibres do not so quickly become exhausted (Burkart). On excitation of the regulator-fibres the respiratory movements become deeper or more superficial in the same ratio as they become slower or quicker, so that the activity of the medulla oblongata remains nearly the same, though it is differently distributed; after section of the vagi, at least, the inspired quantities of gas are on the whole not less (Rosenthal), and the gaseous exchange, at all events at the commencement, is not altered (Voit and Rauber). The inspiratory muscles not in action before irritation of the accelerating fibres are not affected by the irritation, which suspends also the action of those expiratory muscles which happened to be in action before. On the other hand, with the increasing irritation of the inhibitory fibres, the expiratory muscles

¹ Rosenthal, *Die Athembewegungen und ihre Beziehungen zum Nervus Vagus*. Berlin, 1862. 'Ueber den Einfluss des Vagus auf Athembewegungen.' *Archiv f. Anat. u. Physiol.* 1864, 65, 70.

² Burkart, *Pflüger's Archiv*. Vol. i. p. 107.

³ Breuer, *Sitzungsber. d. Wien. Akad.* 1868, Heft 12.

⁴ Traube, *Gesam. Beiträge*. Bd. 1.

will at last come into play (Rosenthal), after the inspiratory movements have ceased.

The accelerating and inhibitory fibres belong to the class of regulator-nerves (for details see Chap. XI.) Different views have already been expressed about the mode in which this regulation is set in motion peripherally during life (Rosenthal, Sklarek, Hering and Breuer). The state of distension of the lungs seems to act mechanically as an excitant of these fibres (Rosenthal); expansion, on the one hand, exciting the inhibitory fibres, which act as expiratory fibres, and contraction, on the other, exciting the accelerating, which act as inspiratory fibres: in this way there would be a sort of self-regulating mechanism presiding over the movements of respiration (Hering and Breuer). The presence of regulator-fibres in the laryngeal nerves also shows that the larynx takes part in this regulation (Sklarek).

Irritation of the mucous membrane of the nose causes for some time an arrest of respiration during expiration; this effect is brought about not by the olfactory nerve, but by the fifth (Hering and Kratschmer). A similar arrest in expiration follows the irritation of many cutaneous nerves, as, for example, the irritation of the cutaneous nerves of the chest on plunging into water (Schiff, Falk).

The exciting cause of the respiratory movements, of which more will be said further on, may either act directly on the medulla oblongata (Rosenthal) or on the terminations of the centripetal nerves going to the medulla oblongata (Rach, v. Wittich), in which latter case respiration would be a *Reflex act*. The decisive experiment—namely, to determine whether all respiratory movements cease after the separation of the medulla oblongata from all its centripetal fibres—has been repeated by both sides with different results. It is, therefore, not possible to come to a decision on this point, as other experiments carried out to support these two views do not agree among themselves.

The exciting cause itself consists in the presence of a certain amount of oxygen and carbonic acid in the blood. The following facts prove that this condition of the blood causes the respiratory movements:—1. The respiratory movements can be totally arrested if, either by a forced artificial respiration (by blowing air into the lung) or by voluntary forced breathing, the blood becomes saturated with oxygen and poor in carbonic acid (*'Apnoea'*). 2. Respiration becomes stronger, and the more accessory muscles take part in it (*'Dyspnoea:'* see Appendix), the poorer in oxygen and the richer in carbonic acid the blood is: as *e.g.* on the entrance of air or fluid into the pleural cavities, causing a collapse of the lungs, or when by inflammation, &c., the lungs are made unfit for respiration. The first respiratory movement in the foetus is in like manner caused by interruption of the respiration carried on through the placenta, which causes a sudden deficiency of the oxygen in the blood, while the carbonic acid accumulates (Schwartz). 3. The same effect will be produced if this alteration in the composition of the blood takes place only locally in the vessels of the

medulla oblongata; ¹ this happens, *e.g.* on stagnation of the blood in these vessels, as after ligature of all arteries going to the brain (Kussmaul and Tenner,² Rosenthal) or on preventing the return of venous blood from the brain (Hermann and Escher), whereby the blood becomes poorer in oxygen and richer in carbonic acid.

A very great deficiency of oxygen destroys the *excitability* of the medulla oblongata, and no irritation whatever, not even a large surcharge of carbonic acid, will again start respiration. This condition is called '*Asphyxia*' (see Appendix).

As almost all the conditions which increase the amount of carbonic acid in the blood are associated with a decrease in the quantity of oxygen, it is difficult to decide whether the want of oxygen or the accumulation of the carbonic acid is the real 'exciting cause' for the respiratory movements. For the present it will be best to look upon both conditions as constituting the 'increased venosity' or 'dyspnœic quality' of the blood (Hering). It is proved that respiration and dyspnœa may be caused by both a deficiency of oxygen without accumulation of carbonic acid (as in the respiration or artificial inflation of the lungs by indifferent gases free from oxygen (H, N, N₂O) (Rosenthal), and also by an accumulation of CO₂ without any deficiency of the O (as in the respiration of air which is rich in CO₂ without being poor in O) (Traube). The argument that in the first case also there is in reality an accumulation of CO₂, because the indifferent gases cannot expel the CO from the blood as completely as O does, and that therefore in both these cases the CO₂ is really the excitant (Thiry), is refuted by the consideration that the respiration of nitrogen causes no accumulation of CO₂ in the blood (Pflüger). We must therefore conclude (Dohmen, Pflüger) either that a deficiency of oxygen by itself, and likewise an accumulation of carbonic acid by itself, may excite the respiratory centre, or (Hermann) that if the CO₂ is alone the exciting cause, its action is the less powerful the larger the amount of O present, just as the action of strychnia, for example, is prevented when the blood is saturated with oxygen: see Chap. XI.

In apnœa the amount of O present is increased in arterial and diminished in venous blood (Ewald); the latter condition is probably produced by a diminution in the velocity of the blood-current in consequence of the great decrease of the arterial blood-pressure (Pflüger).

The phenomenon of Cheyne and Stokes is a peculiar case of abnormal regulation of the respiratory movements: In patients suffering from cerebral and cardiac affections there occurs sometimes an intermittence of respiration; after each pause the respiration increases till dyspnœa is produced, when it gradually sinks again till the next pause. As an explanation it is stated (Traube) that when the excitability of the respiratory centre is diminished, a considerable increase in the venous state of the blood is required each time in order to excite it; the powerful respirations which eventually appear will, however, again considerably diminish the venous state.

Appendix to the Mechanism of Respiration.

The introductory passages concerned in respiration are the nasal apertures, the pharyngo-nasal cavity, the larynx, and the trachea. Respiration by the mouth, although frequently voluntary, as a rule merely serves to replace that by the

¹ This, however, is no criterion for the determination of the question whether the respiratory movements are a reflex act or not; for the advocates of the first view will explain these results by holding the blood of the medulla oblongata to exert an influence in the production of the reflex action.

² Kussmaul and Tenner, *On the Nature and Origin of Epileptiform Convulsions*. New Sydenham Society. 1859.

nose, when the passages of the latter are from any cause obstructed. The above-mentioned channels in part subserve the purposes of respiration by means of suitable arrangements with which they are provided, and in part are the seat of certain movements which are induced in them by the motions of respiration. The inspired air, in passing along them to the lungs, is warmed, and deprived, by contact with the walls, of the coarser solid impurities which it may contain. These particles, as well as superfluous mucus, &c., are driven outwards by the waving cilia which are present on nearly every portion of the walls.

The larynx further possesses in the vocal cords an apparatus for preventing the entrance into the trachea of foreign bodies, such as saliva, small portions of food, &c., as well as of certain irritating gases: for every stimulus causes reflex closure of the glottis. If the glottidean muscles be paralyzed by section of the vagi, or of the inferior laryngeal branches of the vagi, such foreign bodies gain entrance into the lungs easily, and induce fatal inflammations (Traube).

The expulsion of foreign particles which have either found their way into the respiratory passages, or have arisen there as pathological products (mucus), is brought about by the stimulation of the mucous membrane which they cause, and which induces, in a reflex manner, an explosive expiratory blast of air, by which they are driven out. Such explosive expiration is called *sneezing* when the nasal cavities are concerned, and *coughing* when the irritant is in the larynx. Each is accompanied by a noise produced by the sudden bursting open of a closed aperture, which in sneezing is formed by the apposition of the velum palati to the pharyngeal wall, and in coughing by the apposed vocal cords. Coughing may be induced by mechanical irritation of any portion of the respiratory mucous membrane from the lower surface of the upper vocal cords to the alveoli, but it is especially violent when the irritant is applied at the larynx, or at the place of bifurcation of the trachea below (Nothnagel). The sensory nerves implicated in the reflex act of sneezing are the trigeminal nerve, and possibly also the olfactory nerve, and in coughing probably the superior laryngeal branches of the vagi especially. Coughing may also be voluntary. It is quite possible that the bronchial muscles referred to previously (p. 195) may assist in expelling mucus, &c., from the finer bronchial tubes.

Expired air may be used *voluntarily* for purposes similar to those just discussed. For example, mucus may be driven from the nose, the nostrils being voluntarily compressed from without in the process of what is called 'blowing the nose;' or through the isthmus of the fauces, which is narrowed by muscular action, as in 'clearing the throat.' Fluids which it is desired to keep in the throat for some time without swallowing are prevented from entering into the air-passages by keeping up a stream of expired air, which, as it escapes through the fluid in bubbles, causes the characteristic noise of 'gargling.' Warm and moist air expired through the widely-opened mouth may be used for the purposes of heating and moistening. Finally, vocal cords, uvula, tongue, lips, or any of the other apparatuses of the mouth for the purpose of vocalizing, may be set in sonorous vibration, as in 'singing,' 'speaking,' 'blowing.' (Voice and speech are discussed in Chapter VIII.)

If the glottis be closed after a deep inspiration, and the abdominal muscles then powerfully contracted, the viscera of the abdomen become strongly compressed, and such pressure may aid in the expulsion of the contents of the various abdominal organs—rectum, bladder, and uterus (abdominal pressure).

APPENDIX TO CHAPTER IV.

CONSEQUENCES OF A DEFICIENCY OF OXYGEN.

IF by any means the access of oxygen to the blood be prevented altogether, or the quantity entering be diminished in an important manner; or if the oxygen which already exists in the blood be expelled from it or removed in any other way; a group of phenomena can be observed, which ultimately end in death (asphyxia, suffocation).

The oxygen which exists in chemical combination in the blood can be expelled from it by the inhalation of carbonic oxide; further, the oxygen of the blood can be removed by substances which unite with it, as, *e.g.*, sulphuretted hydrogen. The circumstances which, according as they are in full or partial operation, check or altogether put a stop to the oxygenation of the blood, are the following: 1. A want of oxygen in the medium breathed (*e.g.*, prolonged respiration in a limited space of air, respiration in a vacuum or under water). 2. In the foetus, the separation of the placenta or closure of the umbilical vessels before birth. 3. Interruption to the cutaneous or pulmonary respiration, the former by varnish being applied to the skin, the latter by closure of the air-conducting passages. The closure may be due to external causes, as when pressure is applied from without, in strangulation, or to internal causes, such as the following: spasmodic closure of the glottis; obstruction caused by foreign bodies or tumours; accumulation of morbid products, as mucus, in the bronchi; collapse of the lungs by the entrance of air or water into the pleural cavities (pneumothorax, pleuritic exudations); partial destruction of the lungs (as in phthisis); cessation of the respiratory movements; and, lastly, embolism of the pulmonary artery.

When placed in a chamber in which the air is rarified, warm-blooded animals die before the whole of the oxygen has been consumed, in consequence of the evolution of gas within the blood, which leads to disturbance of the circulation (Hoppe-Seyler.) In compressed air death ensues in consequence of the elimination of carbonic acid being hindered (Bert).

With the impoverishment in oxygen which the blood undergoes

under the above-mentioned circumstances, there is generally also an increase in the carbonic acid of that fluid, and these changes in the gases of the blood, as before said, at once cause the respiratory movements to become slower and deeper, under the influence of the *accessory muscles of respiration*; this change in the respiratory movements constitutes *dyspnœa*. Dyspnœa is a regulating act, for in the majority of cases (unless when there is a complete absence of oxygen in the respiratory medium, or when the passage of oxygen to the alveoli is quite impossible) it leads to an increase in the quantity of oxygen contained in the blood, and then itself ceases.

If the impoverishment in oxygen proceeds further, general spasms of all the muscles of the body set in (clonic convulsions); the centre which presides over these is situated in the medulla oblongata, so that we must suppose that the stimulus which leads to normal respiration, if it be increased beyond a certain degree, exerts its action not only on the respiratory, but on neighbouring centres which were normally less irritable. Later on a contraction of the muscular coats of blood vessels occurs which exerts an action upon the heart. This spasm of blood vessels is an intermitting one (Traube), and follows the same rhythm as governs the rudimentary spasms of respiration, which are perceptible even at this stage. (Hering: compare Chapter XI.)

The spasms also occur when the flow of blood to the head is cut off, by ligaturing the carotid and vertebral arteries, and also when an animal loses large quantities of blood (Kussmaul and Tenner); when produced in these ways the spasms have been designated 'anæmic:' their true cause is, however, in all cases, the presence of stagnating blood in the capillaries of the brain—that is to say, of blood which is poor in oxygen and rich in carbonic acid—and they can therefore be produced by preventing the return of venous blood from the brain (Hermann and Escher). Even in the experiment of Kussmaul and Tenner, dyspnœa precedes the spasms (Rosenthal). After hæmorrhage we can readily conceive how stagnation of blood in the vessels of the brain may result in consequence of insufficiency of the propulsive power: it would, however, in this case, be just as easy to suppose that either the want of oxygen or the increase in the quantity of carbonic acid might act as excitants of the substance of the brain.

If the want of oxygen proceeds still further, the irritability of the nerve-centres, which requires for its maintenance a certain supply of oxygen, ceases, and the strongest irritants cannot occasion either movements of respiration or spasms, which, therefore, are in complete abeyance: this condition, which must not be confounded with 'Apnœa' (p. 202), is called 'Asphyxia.' When it has set in, the heart very soon ceases to beat, and death (by suffocation) occurs.

In the state of asphyxia, so long as the heart continues to beat, recovery is still possible (except in cases where the blood has been saturated with carbonic oxide) by distending the lungs with oxygen (artificial respiration). The phenomena which were previously referred to as occurring necessarily during the production of asphyxia then recur, but in inverse order, viz., first of all spasms, then dyspnoea, then normal respiration, and lastly, if air be very energetically introduced, apnoea.

In the dead bodies of asphyxiated animals no difference exists between arterial and venous blood. All the blood of the body is of a dark red colour (this is not the case when death has resulted by the action of carbonic oxide); no oxygen capable of being removed by the usual means is present, and the blood exhibits, when it is examined with the aid of the spectroscope, the absorption band of reduced hæmoglobin; the quantity of carbonic acid is, on the other hand, increased, although not to such an extent as would correspond with the diminution in the quantity of oxygen. The quantity of combined carbonic acid and of nitrogen remain unchanged (Setschenow).

If the blood of asphyxiated animals be shaken with oxygen, a portion of the latter is at once consumed, carbonic acid being formed, apparently in consequence of the presence of easily-oxidised (reducing) substances.

When the deficiency of oxygen persists for a long period, but in a moderate degree, *e.g.*, in cases of partial destruction of lung, as in one-sided pneumothorax, the requirement of oxygen and its supply become adjusted: in consequence, those functions of the body which are associated with oxidation become correspondingly diminished, and the body becomes cooler, more flaccid, the respiratory movements becoming more rapid. Continuous deficiency of oxygen makes itself perceived by the darker colour of the blood, which, aided by a relaxation of the smaller arteries, causes the blue tint presented by the lips, and other mucous membranes, termed *Cyanosis*.

Respiration of Foreign Gases.

In warm-blooded animals the supply of oxygen cannot, consistently with the preservation of life, be dispensed with even for the shortest time: still the oxygen may be mixed with other innocuous gases (hydrogen, nitrogen), as in the atmosphere.

The statement that nitrous oxide (laughing-gas) could replace oxygen for considerable lengths of time (H. Davy) has not been confirmed; pure N_2O causes dyspnoea and asphyxia to occur at once in warm-blooded animals; but in man the former is not perceived, owing to the intoxication it produces (Hermann¹).

The other gases may be classified, in so far as their action on living beings is concerned, in the following manner:—

¹ Hermann, 'Ueber die physiolog. Wirkungen des Stickstoffoxydulgases.' *Archiv f. Anat. u. Phys.* 1864, p. 521.

A. *Indifferent Gases*.—These can, when mixed with oxygen, be respired for an indefinite time without injurious consequences. 1. Nitrogen; 2. Hydrogen; 3. Marsh gas. If inhaled alone, they occasion dyspnoea, spasms, and asphyxia.

B. *Irrespirable Gases*.—These can only be respired when very small quantities of them are mixed with other gases, because in more concentrated states they induce, by reflex action, spasm of the glottis. To this group belong:

a. *Gaseous acids*.—1. Carbonic acid, which being the weakest acid is in the least degree irrespirable, and can therefore be respired in a tolerably concentrated form; when it is respired through tracheal fistulæ it exerts a poisonous action (it therefore has a place under Group C). 2. Hydrochloric acid; 3. Hydrofluoric acid; 4. Hyponitric acid; 5. Sulphurous acid, &c.

b. *Gases which form acids*.—1. Nitric oxide (NO), when mixed with oxygen, at once forms hyponitric acid ($\text{NO} + \text{O} = \text{NO}_2$), and would prove poisonous could it reach the blood (consult Group C). 2. Phosgene gas (chloro-carbonic oxide) COCl_2 , when it comes in contact with water, at once splits into carbonic acid and hydrochloric acid ($\text{COCl}_2 + \text{H}_2\text{O} = \text{CO}_2 + 2\text{HCl}$). 3. Chloride of boron (BCl_3) in contact with water gives boracic and hydrochloric acids. 4. Fluoride of boron (BFl_3) in contact with water gives boracic acid and hydroborofluoric acid. 5. Fluoride of silicon (SiFl_4) under similar circumstances gives silicic acid and hydrofluosilicic acid, &c.

c. *Alkaline gases*.—1. Ammonia; 2. Substitution derivatives of ammonia, as methylamine, &c.

d. *Gases capable of forming substitution compounds or of exerting an oxidizing action*.—1. Chlorine; 2. Fluorine (?); 3. Ozone.

Irrespirable gases can be introduced, through tracheal fistulæ, into the lungs of the lower animals; they generally exert a strongly destructive action upon these organs. Spasm of the glottis is therefore a protective act, and it ceases after the vagi has been divided.

C. *Poisonous Gases*.—These can be respired, but being taken into the blood they lead to injurious or fatal consequences.

This group can be subdivided as follows:

a. *Reducing Gases*.—These become oxidised at the expense of the blood, the oxygen of which they remove; in this manner they lead to the phenomena which are caused by a deficiency of oxygen, dyspnoea, convulsions, and asphyxia. 1. Sulphuretted hydrogen, H_2S , is oxidized in the blood, H_2O and S being formed. As soon as the blood has been freed from oxygen, its hæmoglobin is decomposed, with the formation at first of a body like hæmatin, then of a green substance: these actions do not really go on in warm-blooded animals; for before time for their production has

elapsed, death results in consequence of the removal of oxygen (Hoppe-Seyler, Kaufmann and Rosenthal). 2. Phosphuretted hydrogen (PH_3) is oxidized in the blood, phosphoric acid and water being formed (Dybkowski). 3. Arseniuretted hydrogen, AsH_3 , and; 4. Antimoniuretted hydrogen, SbH_3 , appear to exert a similar action to the preceding. 5. Nitric oxide gas, NO , appears at first to act as a reducing agent (Hermann¹): it is, however, irrespirable. 6. Cyanogen, C_2N_2 , also exerts a reducing action on blood, soon, however, leading to further changes (Rosenthal and Laschkewitsch).

b. *Gases which expel Oxygen.*—These expel the oxygen from its combination with hæmoglobin, and then form a more stable and a brighter coloured red compound; they also occasion the phenomena which are characteristic of a deficiency of oxygen.

1. Carbonic oxide gas, CO . If the blood be not completely saturated with CO , recovery is possible, for the oxygen yet present in blood can oxidize the CO and produce CO_2 (Pokrowsky²).

2. Nitric oxide likewise forms a stable compound with hæmoglobin (Hermann¹): in consequence of its irrespirable nature, it cannot in reality exert this action.

c. *Intoxicating gases, which, when inhaled with oxygen, occasion loss of consciousness and anæsthesia:—*

1. Nitrous oxide gas, N_2O (H. Davy);

2. Chloride of Methyl, CH_3Cl (Hermann);

3. Carbonic acid, CO_2 , leads to a series of complicated phenomena, of which some have already been referred to; it further induces a kind of stupor (Narcosis); the cause of these phenomena is not yet fully understood.

d. *Poisonous Gases, the mode of action of which is not known.*—To this class belong the majority of the remaining gases, which have as yet been very slightly investigated.

¹ Hermann, 'Ueber die Wirkungen des Stickstoffoxydgas auf das Blut.' *Archiv f. Anat. u. Phys.* 1865, p. 469.

² Pokrowsky, *Virchow's Archiv.* 1864, p. 525.

CHAPTER V.

THE EXCHANGES OF THE MATTER OF THE BLOOD.

THE causes of loss and of gain to the blood (expenditure and income) having been considered in the three preceding chapters, the means by which the blood and its constituents remain absolutely and relatively constant must now be discussed.

That under normal conditions of life the income and expenditure of the blood almost exactly balance is proved by the very constant amount (tension) and composition of the blood. Slight fluctuations occur, it is true, even in the normal state, but these are only temporary; an example of such occurs during the time of digestion, when the income decidedly preponderates in amount over the expenditure. It is not yet possible to strike a balance between the income and expenditure of the blood, seeing that as yet it is impossible, even approximately, to ascertain the exact amount of either.

Changes having their seat in the Blood Corpuscles.

It is possible to conceive of changes in the chemical constituents of the blood corpuscles occurring without any simultaneous morphological change. Many facts, however, which will be subsequently referred to, indicate that continually red blood corpuscles are being destroyed, whilst new ones originate. Other facts indicate that the new red corpuscles take their origin in colourless ones.

Tolerably accurate facts are forthcoming in reference to the origin of the latter (the colourless); but far less is known of the place and nature of the transition of colourless into red corpuscles, or at least as to the exact mode of transition.

1. The colourless blood corpuscles are identical with the lymph cells, but probably originate in new-born animals almost entirely in the *lymphatic glands* and *follicles* (as well as in some apparently similarly constructed organs, as the *thymus* and *thyroid glands*), in the *spleen* and the *marrow of bones* (Neumann¹). The cells which are formed in the first-named organs are poured into the blood with the lymph; those which originate in the spleen

¹ Neumann, *Centralblatt f. d. med. Wissenschaft.* 1868, p. 689.

and the marrow of bones, on the other hand (with the exception of those from the splenic follicles, which appear to belong to the lymphatic system), are directly mixed with the blood, in part after being already converted into red corpuscles.

The lymphatic glands and follicles have already been alluded to.

The thymus gland, an embryonic thoracic organ which grows very slowly after birth, and which later in life completely disappears, consists, according to the most recent researches, of *alveoli*, which correspond completely to the lymphatic alveoli and follicles; it also contains products of degeneration (fat cells, amyloid bodies, &c.) Its structure, and the abundant lymphatic vessels supplied to it, lead one to look upon the thymus as an organ similar to the lymphatic glands. In the thyroid body also, according to some (Jeudrassik and, in the case of the frog, Toldt), lymphatic alveoli occur as normal constituents. The cysts which are found in the thyroid filled with colloid masses and crystals of unknown nature, are looked upon as due to a *degeneration*, whilst other vesicles, filled with fluid and lined with epithelium, are looked upon as the normal constituents.

The supra-renal capsules belong to a class of organs of like structure: the areolar tissue of these organs is filled with cells which, by some, are considered identical, or almost identical, with nerve-cells. Concerning their function nothing is known. In consequence of their richness in nerve-fibres and in the above-mentioned cells, some look upon them as a variety of sympathetic ganglia. Others consider them to be connected with the formation of pigmentary matters. In a certain anomalous pigmented condition of the skin (bronzed skin) the supra-renal capsules are diseased (Addison¹), and a violet substance can be extracted from them (Holme).

The structure of the spleen is similarly involved in obscurity (on this subject consult histological text-books). According to the now most generally received conception, the following propositions may be stated:—

1. The *Malpighian vesicles*, which are situated on the sides of the finer arterial twigs, are to be considered as lymph follicles (Gerlach); these form circumscribed thickenings of the arterial wall, and may be considered as simple deposits of colourless (lymph) cells between the separated layers of the adventitia; in many animals this alveolar thickening is not circumscribed, but is more uniformly distributed over the arterial wall (W. Müller).

2. The *splenic pulp* consists, according to some (W. Müller,² Frey), of spaces which are quite similar to the alveoli of the lymphatic glands, except that in the splenic pulp the blood vessels play the same part as the lymphatics in the glands, i.e. the capillaries open into the alveoli, which are filled with lymph cells, and from the alveoli originate the veins. The constituents of the blood thus become mixed with the lymph corpuscles which are there. Besides the red and colourless cells, numerous transition forms between the colourless and coloured blood corpuscles occur in these spaces, and in addition coloured cells and nuclei, which are held to be red blood corpuscles undergoing retrograde changes; these nuclei are in part free, in part enclosed in cell-like masses. Others (Billroth,³ Kölliker, Kyber, Wedl) look upon the blood vessels as forming a system of perfectly closed paths, and explain the apparent admixture as artificial. The splenic pulp has an acid reaction, and, in addition to all the

¹ Addison, *On the Constitutional and Local Effects of Disease of the Supra-Renal Capsules*. London, 1855.

² W. Müller, *Ueber den feineren Bau der Milz*. Leipzig und Heidelberg, 1865. Article 'Spleen,' in Stricker's *Manual of Histology*. Vol. i. pp. 348–364.

³ Theodor Billroth, 'Beiträge zur vergleichenden Histologie der Milz.' *Archiv für Anat. und Physiol.* 1857. 'Zur normalen und pathol. Anat. der Milz.' *Archiv für pathol. Anat.* Bd. xx. & xxiii. 'Neue Beiträge zur vergleichenden Anatomie der Milz.' *Zeitschrift für wissenschaftl. Zoologie*. Bd. xi.

blood constituents, it contains numerous products of oxidation: uric acid, hypoxanthine, xanthine, leucine, tyrosine, inosite, volatile fatty acids (formic, acetic, butyric acids), and lactic acid. It contains, in addition, numerous pigments, an albuminous substance containing iron, and (a fact most worthy of notice) many compounds of iron. The venous blood of the spleen contains an extraordinary number of colourless cells (1 to 70 red, Hirt¹), and the coloured cells found in it are distinguished from others by their smallness, by their being only slightly flat, by their great resistance to the action of water, and by their not having a tendency to arrange themselves into *rouleaux*; these characters are considered to be evidences of their recent formation. In addition, the venous blood of the spleen, like the splenic pulp, contains many transitional forms.

The contractility of the spleen exactly resembles that of arteries; the vaso-constricting nerves of the organ, which correspond to the same class of vaso-motor nerves, run in the left splanchnics and in the splenic plexus (Jaschkowitz); they possess a *tone* which is dependent upon the vaso-motor centre. Asphyxia leads to splenic spasm; direct cold applications also cause the spleen to shrink (Bulgak, Botkin, Mosler, &c.) The influence of the dilatation and contraction of the spleen upon the number of the blood corpuscles in venous blood, and especially upon the number of the colourless corpuscles, has lately been the subject of debate.

Extirpation of the spleen does not necessarily cause death. The function of this organ appears to be capable of being replaced by other lymphatic organs (lymphatic glands, marrow of bones), which enlarge under the circumstances.

The *marrow of bones* contains, in an areolar network, which is quite similar to that of the lymphatic glands, numerous colourless contractile cells, which entirely agree in characters with lymph cells, and, in addition, also transitional forms between these and red blood corpuscles (Neumann,² Bizzozero³). The way in which these cells pass into the blood vessels is not yet ascertained.

The formation of lymph cells in all these organs is, according to the more recent investigations, a process which in its nature agrees with the origin of connective tissue corpuscles. The analogous colourless contractile corpuscles, which are able to wander actively from place to place, and are found in the canal-system of the connective tissue, in the lumen of the lymphatic vessels which originate from this tissue, in the expanded canalicular system of the lymphatic glands and follicles, and, lastly, in the analogous spaces in the spleen, are, we must surmise, constantly being propagated (by a process of fission), so as continually to replace those which pass into the blood (Virchow, v. Recklinghausen).

These views are supported by numerous facts, and, amongst others, by the following:—the presence of lymph cells in lymph which has not yet passed through any lymphatic gland or follicle; further, the pathological formation of lymph cells from undoubted connective tissue cells in leukæmia, a disease in which also the formation of lymph cells in the lymphatic glands or in the spleen (sometimes also in the *medulla ossium*), is morbidly increased; lastly, according to some writers, the formation of pus cells exactly similar to lymph cells by a multiplication of connective tissue cells (Virchow,⁴ C. O. Weber, Rindfleisch, Stricker); this is, however, denied by others (Cohnheim⁵).

¹ Hirt, *De copia relativa corpusculorum sanguinis alborum*. Diss. Inaug. Lips. 1855.

² Neumann, *Centralblatt. f. d. med. Wissenschaft*. 1868, p. 689. And *Archiv für Heilkunde*, 1869, p. 640.

³ Bizzozero, *Centralblatt. f. d. med. Wissenschaft*. 1868, p. 881; and 1869, p. 149.

⁴ Virchow, *Cellular Pathology*. Translated by Dr. Chance.

⁵ Cohnheim, *Virchow's Archiv*. Vol. xl. (1867).

The new formation of colourless blood cells appears to be thus shared by several formative organs, so that one can replace or supplement the other. This conclusion is drawn from the fact that extirpation of any of these organs (spleen, thymus, lymphatic glands, &c.) is followed by no bad consequences to the body, but is compensated for by a vicarious enlargement of the remainder. When, however, several of these organs are extirpated at the same time, life is endangered.

The formation of blood corpuscles in the embryo is quite different from the process which goes on during extra-uterine life. The first blood cells originate with the blood vessels, inasmuch as the innermost layers of the rows of cells which form the latter are directly converted into blood cells and by fission give rise to new ones (Remak, Kölliker). Later on, as soon as the liver is formed, the formation of blood corpuscles is transferred to this organ (E. H. Weber, Kölliker); nevertheless, the process is not clear, nor is the fact itself altogether certain.

Some (Lehmann, Funke) attribute to the liver, during the whole course of life, the function of forming new blood cells, relying chiefly on the richness of the blood of the hepatic veins in colourless cells and in newly formed red corpuscles (similar to those of the splenic blood); nevertheless these observations permit of being otherwise interpreted (see below), and hitherto no follicle-like organs have been detected in the liver.

2. The conversion of colourless into red blood corpuscles appears to occur generally throughout the blood, although it has only been directly demonstrated to occur in the spleen, the venous blood of which contains numerous transitional forms, and in the marrow of bones. The chemical transformation upon which it depends, viz. the origin of hæmoglobin, is unknown; it is affirmed that this substance crystallizes with peculiar readiness in the newly formed red corpuscles (Funke). Hæmoglobin appears to originate under the influence of oxygen, inasmuch as lymph and organs containing lymph are seen to assume a red tint on exposure to air (Virchow, Friedreich). The morphological change consists, according to the received view, in a disappearance of the nucleus, which is followed by a general flattening of the cell, which becomes red; at the same time the corpuscle appears to permit of diffusion taking place into it more and more readily. The young cells, which have just become red, as they are found in splenic and hepatic venous blood, swell but slightly in water, and are not as decidedly flattened as the ordinary, older blood corpuscles, which are easily destroyed by water, are disk-shaped, and are also larger.

In the frog the passage of colourless into red blood corpuscles can be directly observed to occur in blood which has been drawn from the body (v. Recklinghausen¹). The transitional forms which originate in this process are also observed in the circulating blood.

A portion of the colourless cells may possibly not be converted into red, but be destroyed by a process of fatty degeneration (Virchow).

¹ Max Schultze's *Archiv*. Vol. ii. p 157.

3. Little is yet known in reference to the destruction of the red corpuscles. It may be suspected to occur wherever colouring matters originate, as it is probable that these all are derived from blood-colouring matter which has been liberated, therefore especially in the spleen, the liver, the kidney, &c.

Most probably a considerable destruction of red blood corpuscles takes place in the spleen and liver.

In the spleen, if actually the blood is (according to the previously enunciated views) obliged to filter between the colourless cells of the alveoli, many of the cells which penetrate therein with the arterial blood are probably retained. The actual recurrence of such a retention is rendered probable by the following facts:—the traces of substances which are due to the destruction of coloured cells; the shrivelled cells caught in the act of retrograde metamorphosis; the pigmentary matters and ferruginous compounds, and perhaps also the oxidation products; further, the circumstance that the venous blood of the spleen contains only colourless and young red blood corpuscles. The cells which appear to contain blood corpuscles seem to originate by colourless contractile cells taking into themselves red blood corpuscles.

A destruction of red blood corpuscles in the liver appears probable from the fact that the salts of the bile acids possess the power of dissolving the red corpuscles, as well as from the fact that bile pigment is formed; further, from the extremely slow flow of blood through the liver; and lastly, from the poverty of the blood of the hepatic veins in the older red corpuscles. The latter, like the splenic venous blood, contains, as has been already mentioned, only young coloured, and many colourless, cells (Lehmann): from this we may in nowise conclude that a new formation of blood corpuscles takes place in the liver, for the new cells of the splenic vein are conducted to the liver by the portal vein. If we suppose that the 'old' red cells carried by the other radicles of the portal vein are in part or wholly destroyed in the liver, the blood of the hepatic veins must naturally contain a greater number of new elements than the portal blood.

Consequently it appears that a fractional portion of the blood contained in the coeliac and mesenteric arteries loses its red corpuscles, in part directly in the spleen and liver (hepatic artery), in part in the liver (portal vein) only after the stomach and intestines have been supplied. Even in the marrow of bones where pigment and cells containing blood corpuscles are found (Bizzozero; according to Neumann only in pathological conditions) a destruction of red blood corpuscles must occur (Bizzozero).

Exchanges of the Chemical Constituents.

Even less is certainly known in reference to the exchanges of the chemical than of the morphological constituents of the blood. We are acquainted, it is true, in a general manner, as has been explained in the last three chapters, with the constituents which the blood receives and excretes, but we only know approximately the magnitude of this exchange, nor do we know in what manner it is distributed over the various seats of exchange. Further, we know almost nothing on the question as to whether chemical changes of its constituents go on within the blood itself.

The fact that in fresh blood, which contains oxygen, but which is free from carbonic acid, either no carbonic acid or only a mere trace of it is formed, is opposed to the view that oxidation takes

place within the blood. On the other hand, it is usually assumed that the fibrinogenous substance originates either within the blood or in the lymph, from other albuminous substances; but even this is no certain fact, for it is possible that it may be taken up, already formed, from some organ. It is further ascertained that certain easily oxidizable substances, as lactate or caprate of sodium, and glycerin (on the contrary not sugar, or formiate, acetate or benzoate of sodium), when injected into the blood are readily burned, and also when they are made to pass, mixed with blood alone, through any organ; it is, nevertheless, not known whether this process of combustion occurs in the blood itself (Ludwig and Scheremetjewsky ¹).

The exchanges amongst the chemical constituents of the blood which take place during secretion and absorption may shortly be summed up as follows.

1. The gaseous exchanges of the blood have already been systematically discussed in Chap. IV.

2. The inorganic constituents are continually being absorbed in large quantities from the digestive apparatus and from parenchymatous juices, and similarly are being given out to parenchymatous juices and secretions, water besides passing in the process of cutaneous or pulmonary respiration, directly into the atmosphere.

The constancy in the proportion of the inorganic constituents of the blood is maintained by the following arrangements.

A. Water. A diminution of the water of the blood must so influence the exchanges due to diffusion, that, on the one hand, less water is given up by the concentrated plasma to the parenchymatous juices and secretions, whilst on the other hand more water is absorbed. Further, every diminution in the amount of water of the blood is accompanied by a diminution of the volume of that fluid, and therefore by a diminution in the pressure of blood in the vessels, so that less water is given up even in processes of filtration. This effect is most marked in the diminution of the water contained in (and therefore in the amount of) those secretions which are poured outside the body, such as the urine and sweat. In the tissues themselves this effect of a diminished blood pressure is noticeable only in their diminished turgescence.

Finally. Local deficiencies in the amount of water in certain tissues *give rise to specific sensations, which lead to an increased quantity of water being taken with the food* ('Thirst,' Chap. VI.) Conversely, an excess of water in the blood naturally leads to increased excretion by filtration and diffusion, which again is

¹ Scheremetjewsky, 'Ueber die Aenderung des respiratorischen Gasaustausches durch die Zufügung verbrennlicher Molecul zum kreisenden Blute,' *Ber. d. k. sächs. Gesellsch. d. Wissenschaft zu Leipzig*. Vol. xx. (1868) pp. 154-194.

manifested by an increase in the quantity of urine and sweat, and by a cessation of thirst.

Concerning the distribution of water in the body, see Chap. VI.

B. Salts. Even changes in the saline constituents of the blood must modify, as is easily intelligible, the diffusion-exchanges of the blood in such a manner as to lead to an approximate constancy in its saline composition as a whole. We do not, however, know by what means the amounts of the individual salts are maintained constant, or whether a mutual replacement occurs.

3. Organic constituents. As the forces in virtue of which organic substances pass into and out of the blood are as yet quite unknown to us, we cannot surmise the nature of the mechanism, analogous to that alluded to in discussing the inorganic constituents, which maintains them in an approximately constant quantity. We merely know that a continual introduction of organic alimentary substances takes place in consequence of certain mysterious sensations (hunger and thirst), the intensity of which varies with the wants of the system.

The receipt of organic substances into the blood occurs in part without any further change, when they are absorbed from the food without having undergone chemical changes; this is the case with many of the soluble organic constituents of food, with a portion of the soluble albumin (Brücke), and, lastly, with a portion of the fat, which is absorbed into the blood in a state of simple emulsion (F. Hofmann, Röhrig).

The greater number of the alimentary constituents undergo, however, chemical changes in the process of digestion (Chap. III.), and the products of these which are absorbed, appear (after absorption) to undergo further changes before they are converted into constituents of the blood. These changes, which are in great part unknown, are expressed by the term 'assimilation.' The following processes of assimilation have been as yet approximately discovered:

1. Proteids. Gelatin and allied substances are in part converted into peptones before absorption, and in part they are still further decomposed. Inasmuch as peptones cannot be detected in the juices or tissues (Lehmann, Hoppe-Seyler and De Bary) and do not pass into the urine (Fede), they must rapidly be converted into other bodies, presumably into albuminous bodies. Animals can actually be fed with peptones instead of albumin (see page 50).

2. A portion of the fatty matters undergoes decomposition in the intestine, and being saponified, absorption of soaps occurs. Seeing that from soaps taken as food the corresponding fats are formed in the animal body, it is probable that the soaps which are formed in the intestine can, after absorption, be reconverted into fats (Radziejewsky).

3. Sugar, ingested as such or formed in the process of digestion out of starchy constituents of food, is, after absorption, converted into a starch-like substance (glycogen) in the liver (see the Appendix to this chapter).

Seeing that a portion of the albuminous bodies undergoes absorption without a previous conversion into peptones, some suppose that peptones are not reconverted into albumin, but, being burned up so as to furnish urea, are excreted.

The seat of these processes of assimilation is as yet unknown. Many suppose them to occur in the liver, in which organ especially the processes referred to under (3) are to be localised. These processes are, as a whole, synthetic, in opposition to the hydrolytic processes of decomposition which occur during digestion, and of which they are the exact reversals (another synthesis which goes on in the body, that of hippuric acid from glycosine and ingested benzoic acid, apparently occurs in the liver (Kühne and Hallwachs). The process by which the alimentary principles are split up in the intestine (the products of decomposition being, after absorption, employed in synthetic processes, partly in the re-formation of the original substances), is of use from two points of view (Hermann); in the first place, the products of decomposition are in general, on account of their smaller molecules, more easily absorbed than the original substances; in the second place, the products of decomposition furnish a more simple formative material, which alone renders possible the synthesis of the numerous substances which the body requires.

The majority of the complex substances which the body requires must necessarily first arise within it by synthetic processes. As the introduction, with the food, of ready-made hæmoglobin, of undecomposed muscular substance, &c., is impossible, because these bodies are partly decomposed spontaneously, and partly in the alimentary apparatus, it follows that assimilation must require the occurrence of syntheses (Hermann).

In reference to hæmoglobin it has been ascertained that its quantity in the blood is increased by an albuminous diet (Subbotin).

As little is known of the nature of the processes which are concerned in the supply of organic constituents from the blood to the tissues, as of those concerned in the introduction of organic constituents into the blood. Further, the sources are unknown of those blood constituents which are excreted, and especially of those which are excreted in the urine. The latter are by some supposed to take their origin in the liver, because that organ contains more urea than all others, and in the case of birds more uric acid (Heynsius, Stokvis, Meissner); and also because the separated liver gives up urea to blood which is made to circulate through it (Cyon, Gscheidlen); still Munk asserts that the liver contains less urea than the blood.

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Formation of Glycogen and Sugar in the Tissues.

IN many of the animal tissues there occurs a starch-like, or, more correctly, a dextrin-like substance, named *glycogen*, which is very easily converted into sugar by the same means as effect the conversion of starch. This substance occurs principally in the liver (Bernard,¹ Hensen²), in muscles (Macdonell, O. Nasse), in nearly all the tissues of the embryo and of its appendages (Bernard³), as well as in the tissues of young animals, and in newly-formed pathological formations (Kühne). Further, the blood and all the tissues, especially embryonic tissues, contain sugar (Bernard). The amount of sugar contained in the blood amounts to from 0.05 to 0.1 per cent. (Bock and Hofmann, Abeles).

Glycogen appears to occur frequently in small organisms, *e.g.* it is found in the *Ascaris lumbricoides*, and principally in its muscles (Foster⁴). Sugar-forming (glycogenic) substances, which more or less closely resemble the glycogen of the liver, occur also in the brain (Jaffe), in the muscles (dextrin, Limpricht⁵), in many glands (Kühne, Brücke), in blood (Brücke), &c.

Glycogen is obtained from liver by pounding the perfectly fresh organ in sand and water at 100° C., acidulating the fluid so as to completely decompose the alkaline albuminates, filtering and boiling the residue with fresh portions of water until the filtrate is no longer opalescent. The united precipitates are evaporated to half their bulk and precipitated with alcohol, by which the glycogen, mixed with some gluten, is precipitated in white flakes; from the latter it is purified by boiling with caustic potash, neutralising and precipitating with alcohol.

It is more easily obtained free from nitrogenous contaminations by precipitating the aqueous extract of liver by means of a solution of iodide of mercury in iodide of potassium previous to throwing down the glycogen by means of alcohol (Brücke).

Ferments which are capable of converting glycogen into sugar, are not only contained in the sugar-forming secretions (saliva, pancreatic juice) but also in the liver (Bernard⁶), in the blood, and in almost all the tissues (*v.* Wittich,⁷ Lépine⁸). The liver when removed from the body contains large quantities of sugar, which increase as long as glycogen is present.

A question which has not yet been decided is whether the liver contains sugar during life. A perfectly fresh liver taken from an animal immediately after it has been killed contains,

¹ Bernard, 'Sur le Mécanisme physiologique de la formation du sucre dans le foie.' *Comptes Rendus*, 1857, vol. xlv. p. 578.

² Hensen, *Verhandlungen der phys. med. Gesell. in Würzburg*, vol. vii. (1856), p. 219.

³ Bernard, 'Sur une nouvelle fonction du placenta.' *Journal de la Physiologie*, 1859, Vol. ii. p. 31.

⁴ Foster, *Proceedings of the Royal Society*, 1865. No. 79.

⁵ Limpricht, *Annal. d. Chem. u. Pharm.* Vol. lxii. p. 675.

⁶ Bernard, *Leçons sur les propriétés physiologiques et des liquides de l'Organisme*. 1859, vol. ii. pp. 124 and 125.

⁷ V. Wittich, *Pflüger's Archiv*. 1870.

⁸ Lépine, *Ludwig's Arbeiten*. 1870, p. 113.

according to some (Bernard, Kühne), small but yet perceptible quantities of sugar, according to others (Pavy,¹ Ritter, Schiff,² Eulenburg), not a trace. A formation of sugar in the liver during life is further rendered probable by the fact that the hepatic venous blood of animals, fed upon a diet containing neither starches nor sugars, is richer in sugar than the blood of the portal vein (Bernard,³ Tieffenbach); this continuous passage of sugar has been found to be associated with the presence of only a very small quantity of, or even with no sugar in the liver, whilst the very presence of sugar in the liver, and specially its presence in the blood of the hepatic veins, has been denied (Pavy, Ritter, Schiff).

Those who suppose that no sugar is formed in the liver during life, argue either for the presence of a sugar-forming ferment which is only formed after death or in pathological conditions (Diabetes) (Schiff), or suppose that the ferment being present is restrained from exerting its action by a kind of inhibitory influence of the nervous system (Pavy).

The pre-existence of such a ferment in the blood and tissues has lately been contradicted (Lépine, Plósz,⁴ Tiegel⁵). Blood exerts no action on glycogen unless its corpuscles have been destroyed (by the action of water, ether, &c.), so that probably the blood corpuscles generate the ferment at the very moment of their destruction (Plósz, Tiegel). It is worthy of observation in reference to this matter that probably a destruction of blood corpuscles is continually taking place in the liver.

The presence of glycogen in the liver depends very much upon the food. Its amount is large in proportion as the latter is rich in carbo-hydrates (Pavy, Tscherinoff).

¹ Pavy, 'Researches on Sugar Formation in the Liver.' *Philosophical Transactions*, 1860, p. 595. 'Researches on the Nature and Treatment of Diabetes.' London, 1862. 'On the Physiology of Sugar in relation to Blood,' *Medical Examiner*, July 1877.

² Schiff, 'Nouvelles recherches sur la Glycogénie animale.' *Journal de l'Anatomie*. Paris, 1866, vol. iii. p. 354.

³ As this is the general result of Bernard's investigations, and is illustrated by facts narrated in nearly all his papers on the glycogenic functions, the chief and most systematic of these are quoted below:—

a. Bernard, 'De l'origine du sucre dans l'économie animale.' *Archives générales de Médecine*. Paris, 1848, 4me série, vol. xviii. p. 303.

b. Bernard, *Recherches sur une nouvelle fonction du foie, considéré comme organe producteur de matière sucrée chez l'homme et les animaux*. Thèse présentée à la Faculté des Sciences de Paris pour obtenir le grade de Docteur ès Sciences Naturelles. Paris, 1853.

c. Bernard, *Leçons de physiologie expérimentale*. Cours du semestre d'hiver 1854–1855. Paris, 1855.

d. Bernard, *Leçons sur les effets des substances toxiques et médicamenteuses*. Paris, 1857, p. 438 et seq.

e. *Leçons sur la physiologie et la pathologie du système nerveux*. Paris, 1858, vol. i. p. 397 et seq. and vol. ii. p. 544 et seq. (Both these papers refer to the production of artificial diabetes.)

f. Bernard, *Leçons sur les propriétés physiologiques et les altérations pathologiques des liquides de l'organisme*. Paris, 1859, vol. ii. p. 88 et seq.

g. Bernard, 'Sur le mécanisme de la formation du sucre dans le foie.' *Comptes Rendus*. Paris, 1855, vol. xli. p. 461.

h. Bernard, *Leçons sur le Diabète*. Paris, 1877.

⁴ Plósz und Tiegel, 'Ueber das saccharificirende Ferment des Blutes.' *Pflüger's Archiv*. Vol. vii. pp. 391–398.

⁵ Tiegel, 'Ueber die Fermentwirkung des Blutes.' *Pflüger's Archiv*. Vol. vi. p. 249.

In warm-blooded animals which are starved glycogen disappears in the course of a few days, and reappears in large quantities after the injection of sugar into the intestine (Dock). The same result is induced by cane-sugar, milk-sugar, and glucose¹ (Luchsinger), whilst mannite (Luchsinger, Salomon) and inosit (Külz) are without effect. Amongst the substances which lead to an accumulation of glycogen are further to be mentioned, glycerin (Weiss) and gelatin (Woroschiloff); with regard to albumin the statements are contradictory.

The easiest way of explaining the formation of glycogen by the administration of sugars is to suppose that the former is an anhydride formed from the latter. Another supposition considers the proteids as the source of glycogen, this body easily undergoing oxidation in the absence of other bodies, *e.g.* sugar, capable of withdrawing the oxygen from it (Weiss). In support of this view it is alleged that even when glycerin is introduced into the intestine, the liver becomes rich in glycogen. In opposition, however, the easy oxidation of sugar is denied (Scheremetjewsky,² see p. 215, though believed in by Pettenkofer and Voit); further, it is shown that other easily oxidized substances, as sodium lactate, lead to no accumulation of glycogen, and that glycerin only produces that effect when it is introduced into the intestine, and not when it is injected subcutaneously (Luchsinger³). The different kinds of sugar, therefore, and glycerin—which is closely allied to them—appear to be converted into glycogen when they pass through the portal vein into the liver. In support of this conclusion we have the fact that when sugar is injected into the portal vein it does not pass into the urine, as is the case when it is introduced into some other vein (Schöpffer). Even in artificial circulation of saccharine blood through the liver removed from the body, glycogen appears to be formed (Luchsinger).

The destination of the glycogen of the liver is not accurately known. Those who believe that a formation of sugar takes place during life suppose that glycogen is converted into sugar, which is partly excreted and partly burned. Other possible hypotheses as to its destination are the following: that it is carried to other organs which contain glycogen (the muscles, the testicles), and is there consumed; further, that it is converted into other substances, *e.g.* into fats, &c.

Under certain circumstances an abundant excretion of sugar takes place through the urine—diabetes.

These circumstances are: 1. Pathological alterations, the seat and nature of which are unknown to us (pathological diabetes). 2. Injury of a limited space in the medulla oblongata, in the floor of the fourth ventricle (traumatic diabetes, Bernard). 3. The action of certain poisons, especially of curare. 4. The injection of very dilute salt solutions into the blood vessels (Bock and Hofmann). The cause of diabetes may be sought for: *a.* in a con-

¹ Lævo-rotatory glucose causes the same dextro-rotatory glycogen to appear as the dextro-rotatory sugars (Luchsinger).

² Scheremetjewsky, *Ber. d. k. sächs. Gesell. d. Wissensch. zu Leipzig*. Vol. xx. (1868) pp. 154–194.

³ Luchsinger, 'Zur Glycogenbildung in der Leber.' *Pflüger's Archiv*. Vol. viii. pp. 289–304.

version (or increased conversion) of the glycogen of the liver or of other organs into sugar; *b.* in a diminished conversion of ingested sugar into glycogen; *c.* in a diminished destruction of sugar normally originating in the glycogen of the liver.

In pathological diabetes the sugar disappears, almost if not entirely, from the urine, when no carbo-hydrates are taken as food. Even puncturing the floor of the fourth ventricle (*'der Zuckerstich'*) induces no diabetes if the animals have, in consequence of starvation, livers free from glycogen (Dock).

Any existing store of glycogen disappears completely after the diabetic puncture (Luchsinger). The administration of sugar does not cause the liver of diabetic animals to become as rich in glycogen as if they were normal (Dock), though a formation of glycogen still goes on in them; the injected sugar passes, in their case, directly into the urine. The diabetes induced by curare is similarly affected by sugar, as traumatic diabetes (Luchsinger).

The proximate cause of traumatic diabetes has lately been sought for in a paralysis of the blood vessels of the liver (Schiff, Cyon and Aladoff) and of the intestine.

The spot on the fourth ventricle, the puncture of which occasions diabetes, is possibly a portion of the vasomotor centre (Chap. XI.) Even other injuries affecting the vasomotor supply of the liver, *e.g.* injury of the inferior cervical ganglion or of the nerves which proceed from it to the *ganglion stellatum*, occasion diabetes. On the contrary, section of the splanchnic nerves, which probably lowers the blood pressure too much, does not induce diabetes (Cyon and Aladoff). Even diabetes induced by curare may possibly be referred to a vasomotor paralysis. From what has been previously stated vasomotor paralysis should, on the one hand, hinder the formation of glycogen from sugar, or should convert the glycogen (whether stored up in the tissues or newly formed) into sugar, by exerting a hitherto unexplained influence upon the development of the amylolytic ferment; or, more probably, as a consequence of the vasomotor paralysis of the intestine and the liver, the blood circulates so rapidly through the liver that the sugar has not time to be converted into glycogen (Luchsinger). When diabetes follows the injection of dilute saline solutions, the destruction of blood corpuscles may take a part in the formation of the ferment; in these cases the ferment passes into the urine (Plósz and Tiegel). Certain poisons, as arsenic, destroy the power of the liver cells to form glycogen (Faikowsky); consequently injected sugar passes into the urine (W. L. Lehmann, Luchsinger). The same result follows ligature of the common bile duct (Wickham Legg, v. Wittich).

Constancy of the Amount of Blood in the Body.

The constancy in the amount of the blood in the body naturally depends upon the constancy of the different constituents of the blood. As water is by far the principal ingredient of the blood (forming about 80 per cent. of its weight), and as the volume of blood is almost equal to that of the water which it contains, it follows that in the preservation of the constancy of the volume of blood, the constancy in the quantity of water is of the greatest importance: the mechanism concerned in the preservation of the latter has been already discussed. Actually, after great losses of blood, its volume is very soon restored, for, under the diminished blood-pressure, less water is given up to the tissues and to the secretions and more is absorbed, whilst, in addition, increased thirst leads to increased introduction of fluids.

CHAPTER VI.

EXCHANGES OF THE MATTER OF THE BODY, AS A WHOLE.

I. INCOME.

As has already repeatedly been said, the organism receives regularly from without:

1. Food, *i.e.* material for the repair of that which has been excreted either after undergoing oxidation, or in an unoxidized, unaltered condition.

2. Oxygen, for the oxidation of those constituents of the body capable of it. All that is to be said concerning the introduction of oxygen will be found in Chap. IV. Food, on the other hand, here requires a closer consideration.

Food.

The elements of food must in general be the same as those of the body, if they are to serve for the repair of the losses of the latter. Their introduction into the body in an isolated condition is, however, of no value for the purposes of nutrition; because in the case of some of them absorption into the blood is impossible, and in the case of others which are capable of absorption, their elaboration into the chemical compounds which they are to repair is not practicable within the body. As a rule, therefore, chemical compounds alone are capable of use as food, and only in so far as they satisfy the following conditions:

1. The compound must be fit for absorption into the blood or chyle, either directly or after preparation by the processes of digestion (*i.e.* it must be 'digestible').

2. It must replace directly some inorganic or organic constituent of the body; or it must undergo conversion into such a constituent while in the body; or it must serve as an ingredient in the construction of such a constituent. Neither itself nor any of the possible products of its decomposition must be detrimental to the structure or activities of any of the organs of the body (such detrimental bodies are called 'poisons').

Scarcely a single nutritious substance is taken into the body by itself, almost all being ingested, when mixed together in cer-

tain proportions found in nature and called 'Foods,' which are for the most part vegetable or animal tissues, or portions of such tissues. These also are generally further mingled together by artificial means and prepared in various ways, partly to facilitate digestion and partly to render them more palatable.

In the preparation of nutritious material as foods, the most essential process is the addition of so-called 'spices,' that is to say, of substances possessed of such stimulating qualities as render them peculiarly fitted for inducing in a reflex manner the secretion of the alimentary juices (saliva, gastric juice, &c.) The commonest seasoning is salt, which, however, is, in addition, a nutritious body (see below). The preparation of food by boiling, roasting, baking, &c., has for its special object to assist the processes of digestion by anticipating certain of its stages, *e.g.* by dissolving what is soluble, by rendering capable of solution what is insoluble, by loosening the compacter portions, by breaking indigestible skins or husks, &c.

In consequence of what has been said above, all nutritious substances fall into two natural classes, both of which ought to be represented in the food. The first class, which serves for the repair of the unoxidizable constituents of the body, consists of the inorganic elements of food, essentially water and salts; the second, destined to replace the oxidizable portions which are lost, and including therefore bodies which are themselves oxidizable, consists of the organic elements of food. The latter, in common with all organic substances, are derived immediately or mediately from plants; for even the organic constituents of the animal body (forming 'animal food') can be traced back to the vegetable kingdom, as carnivorous animals feed directly or at least in the last instance upon herbivorous animals.

Only a very small proportion of the various organic compounds of C, H, N, O, S, &c., which are formed in plants, really rank as nutritious substances, as many do not fulfil the previously mentioned conditions. The animal substances resulting from the assimilation of such of them as are really nutritious must plainly be capable for the most part of again serving as nutriment; they are the more worthless in this respect the higher the degree of oxidation to which they have attained. That is to say, the value of a nutritious substance is chiefly determinable by the amount of potential energy associated with it; *i.e.* by the quantity of kinetic energy or work which may result from its combustion. The more highly oxidized the nutritious substances, the less is the amount of oxygen which they are in a condition to combine with, and the more incapable are they of furnishing energy to the body. Thus urea has no value as a food, creatine very little, while, on the contrary, albumin and sugar are of the highest importance.

The substances which form the essential organic food of the body would be indicated by considering all the regular constituents of the body as indispensable to it, and inquiring whether they were capable of formation out of any other substance contained in

the animal body; those which were not would of necessity have to be taken into the organism along with the food.

It must, however, here be remembered that in the first place all the substances occurring in the body cannot be regarded as indispensable to it. There is a danger therefore in following the method just given of considering too many nutritious substances as necessary; and a reservation would have to be made on this account. Moreover, it must not be forgotten that a certain number of the constituents of the body cannot be replaced by the introduction of a fresh supply along with the food, either because they are incapable of absorption and indigestible (*e.g.* mucin, keratin, cholic acid); or because they unavoidably decompose before they are ingested (*e.g.* muscle-substance in the act of rigor), or are decomposed in the alimentary canal (*e.g.* hæmoglobin by the acid of the gastric juice); or because they would become rapidly changed—oxidized—after absorption, before they could reach their proper situation. Such substances, therefore, are only produced within the organism.

Our efforts to discover, by the above method, the essential constituents of food are chiefly frustrated by our ignorance of the synthetic powers of the organism. In the preceding chapter it was said that, most probably, in the course of assimilation, albuminous bodies were formed from peptones, fats from soaps (and glycerin), and glycogen from sugar. It is, however, yet unknown whether, for example, the results of the further decomposition of albuminous bodies (leucine, tyrosine, &c.), are capable of synthetic regeneration into albumin. If the organism possessed in general the power of uniting substances synthetically, with the elimination of water, we might briefly indicate the following as necessary organic nutritious substances: viz., the products of the hydrolytic decomposition of all the essential constituents of the body, *i.e.* of the albuminous bodies and their compounds, of the glucosides, of the lecithin-bodies, of fats, &c. These decomposition-products might be contained in food either in an isolated form or already combined into some group, which would in that case be again split up in the course of digestion. The above-mentioned bodies, which have been taken as examples, might therefore be represented in the food in the following ways: (*a*) fatty acids (soaps), glycerin, phosphoric acid, sugar (starch), peptones; (*b*) fats, phosphoric acid, sugar (starch), albumin; (*c*) lecithin, sugar (starch), albumin; or (*d*) protagon, albumin, &c.

The question is still further complicated by the circumstance that we do not know whether, in addition to hydrolytic decompositions, other profounder chemical changes (apart from oxidations) do not take place in the body. Fats especially seem to be capable of originating from other bodies than fats and soaps, for the animal

body may accumulate a large quantity of fat even when the food contains none.

We are guided in the choice of alimentary substances solely by experience, which teaches us that, after water and salts (of which chlorides and phosphates are the chief), albuminous bodies are most indispensable. To what extent true albuminous bodies may be replaced by digestible albuminoids—gelatin and gelatigenous tissues—we shall have occasion to discuss in the third division of the present chapter. It would seem, moreover, that fats (stearin, palmitin, olein, &c.) may only be omitted from the food when the albuminous bodies are present in it in large excess, or when the fats are represented by carbo-hydrates. It is probable, however, that we are not at present acquainted with all the indispensable alimentary substances.

Albumin can, under certain circumstances, be replaced by gelatin or gelatigenous tissues, as the administration of gelatin diminishes the consumption of albumin, so that the body-weight maintains itself on a smaller supply of albumin. As, however, when gelatin alone is administered, in addition to non-nitrogenous food, the body-weight rapidly sinks, we must surmise that the requirements of the tissues for albumin cannot be satisfied by gelatin (Voit). The mean diet for twenty-four hours of individuals in different ranks of society was found by Forster¹ to have the following composition:—

Water	.	.	.	2945.9 grams.	} containing Carbon 312.2 grams " Nitrogen 20.3 "
Albumin	.	.	.	131.2 "	
Fat	.	.	.	88.4 "	
Carbo-hydrates	.	.	.	392.3 "	

The following are among the most important articles of food:

1. Flesh (muscle) contains, besides water and salts (especially of potassium) amongst the more essential nutritious elements (Chap. VIII.), several albuminous bodies (myosin, albumin), gelatinous tissues, small quantities of lecithin (possibly derived from the intra-muscular nerves), fats and certain 'extractive matters,' some of which are agreeable to the taste ('osmazome'), while others seem to have weakly stimulating properties (creatine, &c.) It is ingested raw, boiled with water, or roasted. After boiling, the extract—broth of meat—contains chiefly the gelatin, the extractive matters, the salts (which on account of the potassium they contain cause concentrated broths to have an important effect upon the heart (Kemmerich), and some of the fat floating on the surface. The albuminous bodies are insoluble in hot water, and remain behind in meat which is immersed at once into *hot* water; if *cold* water be used, the albumin passes into the water, coagulates as the latter becomes heated, and is removed with the 'scum.' The flesh which remains behind after the removal of the broth still retains most of the nutritious constituents (myosin and the gelatigenous tissues, and albumin if the water used were hot to commence with), but has lost its salts and those bodies which gave it an agreeable flavour. Meat which has been roasted, *i. e.* strongly heated with the addition of little or no fluid substance (water or fat), retains all its constituents; and certain brown, empyreumatic bodies possessed of an agreeable taste and smell are formed in it especially at the surface.

2. Milk contains albuminous bodies (albumin, casein), fats (butter), and probably lecithin, besides carbo-hydrates (milk-sugar), water, and a considerable

¹ 'Beiträge zur Ernährungsfrage.' *Zeitschr f Biologie*. Vol. ix¹ (1873) pp 381–410.



quantity of salts. It may be ingested fresh or sour; or the butter alone may be taken; or the cheese alone. Cheese, however, or the casein precipitated on the acidification of milk, whether occurring spontaneously or on the addition of 'rennet' (the mucous membrane of the calf's true stomach), includes a considerable amount of fat. On standing, cheese undergoes a change similar to that of digestion, becoming soft and translucent owing to the formation of peptones and the further decomposition of casein. This is called 'ripening,' in the course of which fat is said to be formed out of casein, and leucine and tyrosine to appear.

3. Eggs. The white of egg contains a concentrated solution of albumin, while in the yolk are found albuminous bodies, much lecithin, cholesterin and fats, and sugar. On heating, the white coagulates firmly, the yellow into a mass which readily crumbles.

4. Cereals (wheat, rye, maize, barley, rice, oats, &c.) contain an albuminous body (gluten, vegetable fibrin, insoluble in water), an albuminoid (vegetable gelatin), lecithin (Hoppe-Seyler), traces of fat, starch in large amount, and especially at the time of germination, an amyloid ferment (diastase). Grain which has been ground and freed from the husks (bran) is called flour or meal, and is chiefly used in the preparation of bread. On mixing flour with water a tenacious mass, *dough*, is formed by the action of the latter on the gluten. This dough must be then loosened or rendered spongy, and afterwards heated strongly. The loosening is effected by the evolution in the dough of carbonic acid gas, produced by the conversion of part of its starch, by means of the diastase, into dextrin and sugar, and the fermentation (alcoholic) of the latter on the addition of barm or yeast. The dough thus caused to 'rise' is then heated to about 200° C., which serves to drive off the alcohol at once. The plan of introducing artificially prepared carbonic acid into the dough instead of evolving it by means of fermentation has recently been adopted (aërated bread). Another substance derived from cereals is beer, a watery decoction of grain (malt) which is germinating, and therefore rich in dextrin and sugar. Yeast is added to the decoction, which thereupon undergoes alcoholic fermentation. Beer contains chiefly dextrin, alcohol, bitter substances which are added to it, and absorbed carbonic acid. Of all intoxicating liquors it is the one which contains least alcohol (2-8 p.c.) On distillation, beer and similar fermented liquors prepared from malt (or potatoes) yield a beverage (brandy) very rich in alcohol.

5. Leguminous fruits (peas, beans, lentils, &c.) contain a great quantity of an albuminous body (legumin), besides lecithin and starch. They are eaten for the most part after having been boiled in water, the starch being therefore in the form of a paste. It is not possible to use them in the preparation of bread, as on account of the absence of gluten they do not form a dough.

6. Potatoes chiefly contain starch, in addition to a small quantity of albumin.

7. Fruits which are sweet contain various kinds of sugar, dextrin, vegetable gelatin, very little albumin, and organic acids (tartaric acid, malic acid, citric acid, &c.) Many species, especially grapes, furnish alcoholic beverages—wines—on fermentation of their juices.

8. The green parts of plants (leaves, stalks, &c.), and roots, contain chiefly starch, dextrin, sugar, and albuminous bodies in small amount.

All vegetable alimentary substances contain, as their chief constituent, cellulose, which is almost or entirely incapable of digestion by man and carnivorous animals, but which is probably of great nutritive value to herbivorous animals.

Ingestion of Food.

The ingestion of food takes place voluntarily, at intervals which are, for the most part, of such short duration that digestion and absorption are scarcely interrupted, at least during the day.

It receives its stimulus in certain sensations—hunger and thirst—which have not hitherto been satisfactorily explained, but which indicate the lack of nourishment on the part of the organism. The sense-organs in which this necessity of the whole body makes itself felt as sensations are certain parts of the alimentary apparatus. Thirst alone takes the form of a localised sensation, a feeling of dryness and burning in the throat, occasioned by deficiency of water in the mucous membrane of the palate and pharynx. This deficiency of water is usually only the local manifestation of the general state of the tissues of the organism. It may, however, be induced by drying the mucous membrane of the throat (by blowing dry air over the part), or by withdrawing the water in some other way (by the application of hygroscopic salts). The feeling of thirst may be allayed as a rule by the local application of water to the parts concerned; and, as this is accomplished most frequently by drinking, the whole body is at the same time supplied with water. Other methods of introducing water into the system, *e.g.* its injection into veins, also allay it, as would be expected from the circumstance that it results from the general deficiency of water in the tissues (Chap. X., Sec. v.) Hunger, on the contrary, which is a pressing, gnawing sensation in the stomach, and, in its later stages, in the intestine also, cannot be regarded as the local expression of a general lack of nutriment occasioned by deficiency of material in the neighbourhood of the gastric and intestinal membranes. It is, as it seems, a sensation of emptiness in the digestive organs, the conditions of which are yet quite unknown; for it may be assuaged by filling the stomach, even though it be with indigestible matter. In such a case, of course, a sensation of general lack of nourishment supervenes after a time, which differs from the usual feeling of hunger, but the nature of which is as little understood.

The nerves which minister to the sensation of thirst are probably some or all the afferent nerves of the palate and pharynx (fifth, vagus, and glosso-pharyngeal). Those concerned in hunger are yet quite unknown. Section of the vagi and of the splanchnics does not diminish the desire for food in animals.

II. LOSSES.

The substances which the body is continually giving up as of no further use to it are:

1. Substances which are quite incapable of taking part in the exchanges of matter, *viz.* the indigestible portions of food.
2. Those results of the oxidations occurring in the body which are incapable of any further oxidation while within the body, *viz.* carbonic acid, water, urea, and uric acid.
3. Certain secreted materials which have been poured out on

the internal or external surface of the body in order to be utilised there, and which, on account of some property, are incapable of reabsorption, *e.g.* the insoluble constituents of bile, the mucus of the alimentary secretions, the fats of the tegumentary secretion, horny substance, &c.

4. A portion of the unoxidizable constituents of the body—water and salts—which are continually excreted, owing to their physical deportment towards other bodies; for example, water is excreted for the most part as the solvent of other excretory substances.

The above-mentioned substances may be got rid of in the form of gaseous, liquid, or solid excretions. The most important are:

1. The respiratory excretion from the lungs, skin, and intestine (carbonic acid and water).

2. The urine (water, salts, urea, uric acid, &c.)

3. The fluid tegumentary excretions, viz. sweat (water, salts, urea, fatty acids, &c.), and the sebaceous excretion (fats, water, salts, albumin).

4. The fæces (the indigestible portions of food and of the alimentary secretions).

5. The exuviation of epithelium (the shedding of epidermis, hair and nails).

In addition to the above-mentioned excretions, which contain for the most part really excrementitious substances, the body yields up periodically certain of its constituents which are so little oxidized as to be capable of further use in the formation or nourishment of other organisms. They are: 1, Milk; 2, Ova; 3, Semen; which are excretions rich in albumin, carbo-hydrates, and fat. Menstrual blood may also be included in the list.

Most of the excretions above referred to are direct secretions from the blood, and, as such, have been already described. Thus urine, the sudoriparous and sebaceous excretions, and milk, are treated of in Chapter II., and the respiratory excretion in Chapter IV. Fæces, or the mixture formed in the alimentary canal during digestion, have been mentioned in the description of that process in Chapter III. The remaining excretions, viz. those of epithelium, ova, and semen, consist essentially in the separation of cells or portions of cells. The last two are discussed in the Fourth Section of the book. The exuviation of epithelium takes place in the following manner:—Those internal and external surfaces which are covered with scaly epithelium, viz. the epidermis, the mucous membrane of mouth and pharynx, portions of the urinary and genital organs, and the conjunctiva, lose continually their upper layers of cells after the latter have undergone a peculiar process of shrinking and conversion into a horny material. The horny cells of the external skin, *i.e.* the most external layers of the epidermis, together with the corresponding portion of nails and hair, are simply rubbed off by use; those of the mucous membranes mingle

in the secretions which bathe them (saliva, mucus, urine, tears), and are conveyed out of the body in the fæces or urine as the case may be. This desquamation of epithelial cells is the cause of no inconsiderable loss of nitrogen and sulphur to the body.

III. THE ECONOMY OF THE BODY.

1. *When the Gains are equal to the Losses.*

The simplest relationship which can exist between the food consumed and the body is, when the former is just sufficient to cover the expenditure of the latter, and so to maintain it at its usual standard of weight. In this case it is not, of course, sufficient that the total gains of the body equal the total losses. If the chemical composition of the body is to remain unchanged, the amount of the individual chemical constituents of the former must also be equal to the corresponding constituents of the latter. When this is the case the following relations exist between Gains and Losses :

1. The total losses of the body, after subtracting the fæces which are most variable in quantity, are referable in about an equal extent to the urine on the one hand, and to the sudoriparous and respiratory secretions on the other. In this division the following are neglected : the true elements of loss contained in the fæces (constituents of bile, &c.), the sebaceous secretion, and the exuviated epithelial cells, concerning which no determinations have as yet been made. In carnivorous animals the urinary secretion is for the most part somewhat in excess of all the others, including the fæces. In herbivorous animals, on the contrary, it only amounts to one-eighth or one-third of the other secretions. The cause of this lies chiefly in the greater amount of fæces excreted by the latter.

2. The elements which compose the inorganic constituents of the body (water and salts), and which are excreted and restored in similar combinations, are the following :

- a.* Water. The proportionate amounts of water separated by the various excretions, if we except that separated in the fæces, which is generally of small amount, depend chiefly upon the temperature and the hygrometric state of the atmosphere. The loss of water from the lungs is almost constant, as there the same extent of surface moistened to the same degree constantly comes into contact with the atmosphere by means of a stratum of air which is continually in motion. Moreover, the loss of water by cutaneous respiration cannot be distinguished from that which occurs in the secretion of sweat; hence, both may be taken together. Therefore, it may be said that the chief loss of water is referable to the lungs, skin, and kidneys. For reasons which are very apparent, it will be seen that with a dry, warm atmosphere,

the loss of water from the skin will be greater than that from the kidneys, while with a moist, cold atmosphere, the reverse will obtain. That the total amount of the excreted water depends upon the amount ingested has already been indicated: and more will be said below in reference to this matter in speaking of the ingestion of excessive amounts of food. In carnivores almost the whole of the water (as much as 90 per cent.) is got rid of from the kidneys; while in herbivores as much as 60 per cent. passes away in the fæces.

b. Salts are chiefly excreted in the urine; some, however, appear in the sweat, while a few (mostly those of potassium and the indigestible salts) pass out of the body in the fæces, together with any superfluity of salts which may have been ingested.

3. The elements of the (oxidized) organic compounds of the body are excreted for the most part in the form of inorganic products of oxidation, and less frequently as organic products of oxidation or decomposition. They are:

a. Carbon, by far the largest portion (more than 90 per cent.) being excreted in the form of carbonic acid in the process of respiration. A smaller amount is separated in the form of less highly oxidized products during the other processes of secretion (in urea, uric acid, &c.; in the horny substance of epithelium, the sebaceous secretion, the constituents of the secretions contained in the fæces, &c.)

b. Hydrogen (*i.e.* that derived from the organic constituents of the body) is separated for the most part in the form of water, together with the water which previously existed as such in the body. A small portion quits the organism in the organic compounds mentioned under *a.*

c. Oxygen (*i.e.* that derived from the organic compounds of the body) is excreted together with that taken into the system for the purposes of oxidation, the amount of the latter kind being from three to ten times as great as that of the former. By far the greater proportion is separated in the most highly oxidized bodies highest forms of oxidation, viz. as carbonic acid and water, only a small amount being excreted in the less oxidized bodies as urea, &c.

d. Nitrogen is excreted entirely in the form of decomposition-products, for the most part as urea in urine and sweat, but also as uric acid, urinary colouring matter, horny substance, biliary constituents, and possibly in small amounts, as ammonia and pure nitrogen.

The old question whether, when the body-weight remains the same, all the nitrogen taken into the system reappears in the visible excretions (especially in urine and fæces), or whether a part only is so excreted—a circumstance which would compel the admission of a separation of nitrogen in the lungs—seems now to have been settled in favour of the former alternative (Voit, Siewert, Schulze and Märcker [Henneberg], Stohmann: this view is, however, opposed by Seegen). In the special case where the food happens to be very albuminous,

it is still maintained by Stohmann that the amount of nitrogen recoverable from the visible excretions is less than that ingested. When cutaneous perspiration takes place such a comparative deficiency of nitrogen is observable owing to the excretion of that body in the sweat (Leube).

e. Sulphur (derived especially from the alkaline albuminates of the body) leaves the organism, about half of it in the form of sulphates in the urine, and the rest, combined in various organic compounds, in epithelial exuviations and in the fæces (keratin, taurine).

The question of how much food must be taken, in order that the gains and losses shall balance, cannot be answered simply. Seeing that the organism on account of its indispensable activities, and the tissue changes which necessarily accompany them, is subject to certain necessary losses, it might appear as if two ways would lead us to our end. The first would consist in giving a man or an animal the smallest amount of food requisite for the maintenance of the weight of the body, and in analysing the excreted substances under these conditions, the elements of which should correspond quantitatively with those of the food: the second, in depriving an animal of all food, in which case we may be certain that no material is unnecessarily excreted, and then determining the necessary elements of food by analysis of the excreta. Both methods are, however, very defective, and experience teaches that the same individual is able to maintain a state of nutritive equilibrium on very diverse amounts of nutriment—that, in fact, the losses and stock of the body regulate themselves according to its gains, as will be shown in the sequel.

The first method possesses the following sources of error: 1. The process itself is a working in the dark, and leads with difficulty to an exact result. 2. The difficulty of excluding all unnecessary use of material such as would be occasioned by movements, &c. 3. The uncertainty whether the amount of food which is just sufficient to maintain the weight of the body at its normal, would not be found to be less if its composition were more judiciously arranged; or, in other words, whether certain of the constituents of the excreta are not due to an excess of the materials ingested. 4. The difficulty in estimating the elements of the fæces. The fæces contain (Chap. III.) not only the results of material exchanges (portions of the alimentary secretions), but also the indigestible parts of food, which must by no means be reckoned among the losses of the body due to the repair of its tissues, but are to be attributed to the accidental composition of the food itself. The fæces of herbivorous animals, for example, form almost the half of the total excretions of the body (in horses 40 to 50 per cent., Valentin, Boussingault; in cows, 34·4 per cent., Boussingault) on account of the considerable quantity of indigestible material contained in vegetable food. In carnivorous animals, on the contrary, the proportion is very unimportant (in cats 1 per cent., Bidder and Schmidt). In omnivores it is intermediate (being in men 4 to 8 per cent., Valentin, Barral, Hildesheim; and in pigs 19·9 per cent., Boussingault), and varies from time to time with the kind of food. In order to eliminate this very varying and unnecessary factor in the calculation of the losses of the body, we must either disregard the fæces altogether—in doing which another error is introduced by overlooking the real elements of loss which they may happen to contain—or we must choose alimentary substances which contain no indigestible portions—an experiment which has not yet been tried.

In the second method a great error is introduced by the circumstance that in famished animals the various functions quickly become languid, and, in consequence, the consumption and the losses of the body less than when a sufficiency of food is taken.

The data concerning the absolute amount of the losses of the body and the quantity of food necessary to repair the losses are therefore very uncertain. The following is an epitome of the results which have been obtained :

1. The minimum excretion (or ingestion) is larger the smaller the animal observed. For the purposes of comparison, the exchange of matter, in twenty-four hours, per kilogramme of the weight of the animal, is determined. It is thus found that in pigeons a far larger exchange of matter occurs for every kilogramme than in dogs ; while in the latter it is far greater than in man. This is explained by the greater activity of the vital processes in smaller organisms : small animals, for example, on account of the comparatively large extent of surface which they expose, must generate more heat than large ones, in order to maintain their temperature (Chapter VII.)

2. The minimum amount of food necessary is lowest when the elements of the food are mingled together in a definite manner. Such a perfect mixture of the elements of food contains proteids, fats or carbo-hydrates, possibly also lecithin, water and salts in certain proportions, the salts being present in smallest amount, and water in greatest.

3. The most favourable relationship of these elements one to another, *i.e.* the proportion that must exist among them so that the smallest amounts may be able to maintain the normal weight of the body, varies in the varying conditions of age, sex, and mode of life.

4. Up to a certain point the amount of albumin usually considered necessary in the food may be decidedly diminished by increasing the amount of fats or carbo-hydrates : possibly, as Hoppe and Voit suggest, because every body which oxidizes more easily than albumin prevents the action of oxygen on that body by attracting it to itself.

5. The minimum amount of food necessary is greater according as the organism is already fattened by excessive feeding.

The absolute numbers which represent the minimum bodily exchanges, determined according to the methods previously referred to, in consequence of defects inherent in the methods, only possess value when all the conditions of the experiment are carried out. Here their function ceases. We must, however, mention that the temperature, the amount of muscular work, &c., also influence the material waste of the body.

As an example of the receipts and losses of a strong man in a condition of almost exact nutritive equilibrium, the following tabular statement (Pettenkofer and Voit) is appended :—

Weight at the commencement of the experiment . . . 69.29 kilos.
„ after completion „ „ . . . 69.55 kilos.

Grammes in 24 hours.		Water	C	H	N	O	Mineral matters
GAINS :							
Meat	139.7	79.5	31.3	4.3	8.50	12.9	3.2
Albumin	41.5	32.2	5.0	0.7	1.55	2.0	0.3
Bread	450.0	208.6	109.6	15.6	5.77	100.5	9.9
Milk	500.0	435.4	35.2	5.6	3.15	17.0	3.6
Beer	1025.0	961.2	25.6	4.3	0.67	30.6	2.7
Melted fat	70.0	—	53.5	8.3	—	8.1	—
Butter	30.0	2.1	22.0	3.1	0.03	2.8	—
Starch	70.0	11.0	26.1	3.9	—	29.0	—
Sugar	17.0	—	7.2	1.1	—	8.7	—
Salt	4.2	—	—	—	—	—	4.2
Water	286.3	286.3	—	—	—	—	—
Inspired oxygen	709.0	—	—	—	—	709.0	—
		2016.3 =	—	224.0	—	1792.3	—
Sum of the gains	3342.7	—	315.5	270.9	19.47	2712.9	23.9
LOSSES :							
Urine	1343.1	1278.0	12.60	2.75	17.35	13.71	18.1
Fæces	114.5	82.9	14.50	2.17	2.12	7.19	5.9
Expired products	1739.7	828.0	248.60	—	—	663.10	—
		2189.5 =	—	243.30	—	1946.20	—
Sum of the losses	3197.3	—	275.70	248.22	19.47	2630.20	24.0
Difference—Gains minus losses	+ 145.3	—	+ 39.8	+ 22.7	0	+ 82.7	−0.11

2. When the Supply of Food is Deficient.

Inasmuch as the indispensable activities of the body, as the movements of the heart, and of respiration, and the development of heat, are constantly accompanied by certain losses, it follows that, if the body be supplied continuously with an insufficient diet, a time must come when the body-weight will commence to decrease, the loss of weight continuing until death. In the case of starvation, when there is a complete deprivation of food, this diminution in body-weight commences at once; and sooner or later, according to the condition of the animal at the commencement, a period arrives at which the functions of the body, as well as its losses, begin to diminish; this diminution continues until death. The material exchanges which occur in fasting animals merely consist

in the combustion of the constituents of the body by means of the oxygen continually inspired, and the excretion of the products of that combustion, and of the incombustible constituents, water and salts. The organism, as a whole, undergoes in the meantime no repair; but, in all probability, certain portions of it are restored at the expense of others by the action of the blood, which transfers to the former the energy-yielding materials which the latter may contain in superabundance.

Observations of the material exchanges of fasting animals (Experiments on Inanition) extending over considerable periods have only been made on the lower animals, chiefly on pigeons (Chossat), dogs (Bischoff and Voit), and cats (Bidder and Schmidt).

The following generalizations have been made from experiments on fasting animals:

1. At the beginning of the process of starvation the body-weight as well as the activities and the losses of the body decrease. The diminution in the losses of the body naturally causes the decrease in its weight to become less from day to day; for the sum of the losses or excretions, after subtracting the amount of the oxygen taken into the body, expresses directly the loss of the body in weight. The diminution in the bodily energies or activities, which is intimately connected with the decrease in the losses, is indicated especially by a low temperature and an infrequent pulse and respiration, the diminished income of oxygen thus brought about occasioning a diminution in the processes of oxidation.

2. The diminution in the excreta does not affect all their elements equally. Herbivores exhibit the most considerable alteration in the composition of their excreta; for all fasting animals may be regarded as carnivores, since they subsist on nothing but the constituents of their own bodies. Thus, in the case of fasting herbivores, the amount of urea in the excretions at first increases. As a rule, however, the amount of urea in the excretions diminishes as the time during which no food has been taken extends—a proof that the decrease in the processes of oxidation in the organism concerns also the oxidation of the nitrogenous (albuminous) constituents of the body. The diminution in the amount of urea excreted is at first abrupt, and the more so the larger the amounts which were normally excreted before starvation commenced; later on, the excretion of urea diminishes slowly and regularly. While, therefore, in the later periods of starvation, a certain proportion of the albumin of the body (organic albumin) is regularly used up, at the commencement it is the stored-up albumin derived from the food last ingested which is expended (Voit).

3. After the animal has lost a certain fraction of its weight,

death by starvation supervenes, the interval from the commencement of starvation varying in different individuals. The length of the interval, and the amount of the loss which the animal is able to sustain before death, depend upon the condition of the animal previously. Animals which have been fattened require a certain time longer to allow of their weight attaining its normal condition; for not until this has been accomplished does any diminution in the losses and activities of the body occur, and starvation, therefore, really commence. Thus, young and poorly-fed pigeons die in three days, after losing one-fourth of their weight, while old and well-fed birds will live for thirteen days, until they have lost nearly the half of their former weight (Chossat).

4. The amount of loss in weight determined after death differs much in various parts of the body. The oleaginous contents of the fatty tissues (or, briefly, the fat) diminish most, the whole tissue losing from 91 to 93 per cent., *i.e.* the connective tissue alone remains. The abdominal viscera and muscles lose less weight than the fat. The brain and spinal cord lose extremely little; the former, however, somewhat less than the latter. The blood, it may be noted, especially in the amount of its hæmoglobin, maintains approximately its relationship to the whole weight of the body. This inequality of loss in the various parts of the body is brought about by the power, before referred to, which the blood has of conveying material from one organ to another, and thus securing as perfectly as possible, the nourishment of the organs most frequently used. This is indicated not only by the fact of the slight loss of weight of the brain, the activity of which continues undiminished until death, but also by the smallness of the loss sustained by those muscles which are continually in use, as compared with the loss sustained by those which are less active. As fat and muscle are the chief elements in the losses of animals when fasting, it is generally stated that animals in such a condition live upon their own fatty and muscular tissues. Certain investigators (Schmidt, Bischoff and Voit) have even calculated from the nitrogenous elements of the excreta the quantity of such muscular substance used, and have considered all the remaining elements which are referable to the organic constituents of the body (calculated from the carbonic acid excreted) as derived from consumed fatty material.

In addition to the case of total deprivation of food, we must consider that in which food is administered in insufficient quantity. This insufficiency may be quantitative or qualitative, *i.e.* the food taken may contain all the necessary elements of food, but in insufficient quantities, or it may not contain all the essential elements. Quantitative insufficiency induces all the symptoms of complete starvation, but much more slowly. Qualitative insufficiency in most cases terminates in death as quickly as complete starvation, but with a less diminution in the body-weight. During

complete deprivation of water¹ (Schuchardt) animals very quickly cease to take solid food; and, on the contrary, during complete deprivation of the solid constituents of food (Bischoff and Voit, Chossat), they very soon refuse to take water: each, therefore, may lead to starvation. In many combinations of the alimentary elements in food, the observations are interfered with, either by the fact that the maximum absorption becomes so slight that it is impossible to study the effects of large amounts, or by the appearance of morbid symptoms, *e.g.* of diarrhoea when the combination consists of sugar and water. Those experiments are of most importance in which one of the two chief organic alimentary substances, albuminous bodies or fats (carbo-hydrates), is withheld from an animal. In such cases the general loss to the body is considerably less than in fasting animals; each of these elements of food, therefore, can to some extent replace the other. On withholding the albuminous elements (as by feeding on fat and water, or on fat, carbo-hydrates and water) the excretion of urea becomes considerably decreased, while the weight of the body undergoes a certain but not excessive diminution, indicating that the oxidation of nitrogenous bodies is proceeding less rapidly than usual within the organism. On withholding fats, no marked alteration in the exchanges of matter of the body occurs if the food contain carbo-hydrates in their place. If the latter are also withheld, a very decided increase occurs in the excretion of urea, indicating an increased oxidation of nitrogenous materials, and necessitating an increased ingestion of nitrogenous food in order that life may be maintained.

3. *When the Supply of Food is Excessive.*

The matter which the body gains is in greatest part taken voluntarily, and without its amount being regulated by any accurate knowledge of the requirements of the organism; for the sensations which might give expression to these requirements, *viz.* hunger and thirst, lead in general only to food being taken, not to its being taken in a regulated quantity, and besides, very often food is taken without the intervention of either hunger or thirst. Hence the consumption of a diet exceeding the wants of the body is very usual—indeed, the rule. This, too, depends upon the fact that up to a certain age the body is continually increasing, and that after that age certain losses of unoxidized materials occur in both sexes (semen, menstruation, nutrition of the embryo, lactation).

In the case of a very abundant diet, the following events might be conceived to occur:

¹ That is to say, of that also which is contained in the organic alimentary substances; for many animals (*e.g.* cats, Bidder and Schmidt) can do very well without actually drinking water.

1. The substances taken in excess of the requirements might not be absorbed, but be excreted unchanged in the fæces;—this event occurs only when the excess is very great; the maximum amount of absorption will be soonest reached in the case of salts, then in that of fats, and last of all in the case of water; or the substances in excess may be absorbed, but immediately afterwards excreted without having undergone any changes: this occurs only in the case of water and salts, which are excreted until the body has its normal amount of these substances left: unoxidized *organic* bodies do not under normal circumstances occur in any excretion excepting in milk, in ova, and in semen.

2. The substances in excess might be simply retained, and the losses continuing the same the weight of the body increase; in this case the store of potential energy of the body would be added to.

3. The excessive ingestion might be followed by an increase in the decomposition, in the processes of oxidation, and in the activities of the body, so that the losses increased and the weight of the body remained unchanged.

4. Were it conceivable that without any increased oxidation the weight of the body were able to remain approximately constant,—and that a decomposition of the substances taken in excess occurred, leading to the formation of certain products of decomposition very rich in potential energy, and of others very poor, of which the former were retained and the latter excreted—then the potential energy associated originally with all the matter in the food taken would be concentrated in a smaller amount of matter, so that a marked increase in the store of energy of the body would occur, but only a slight increase of its weight.

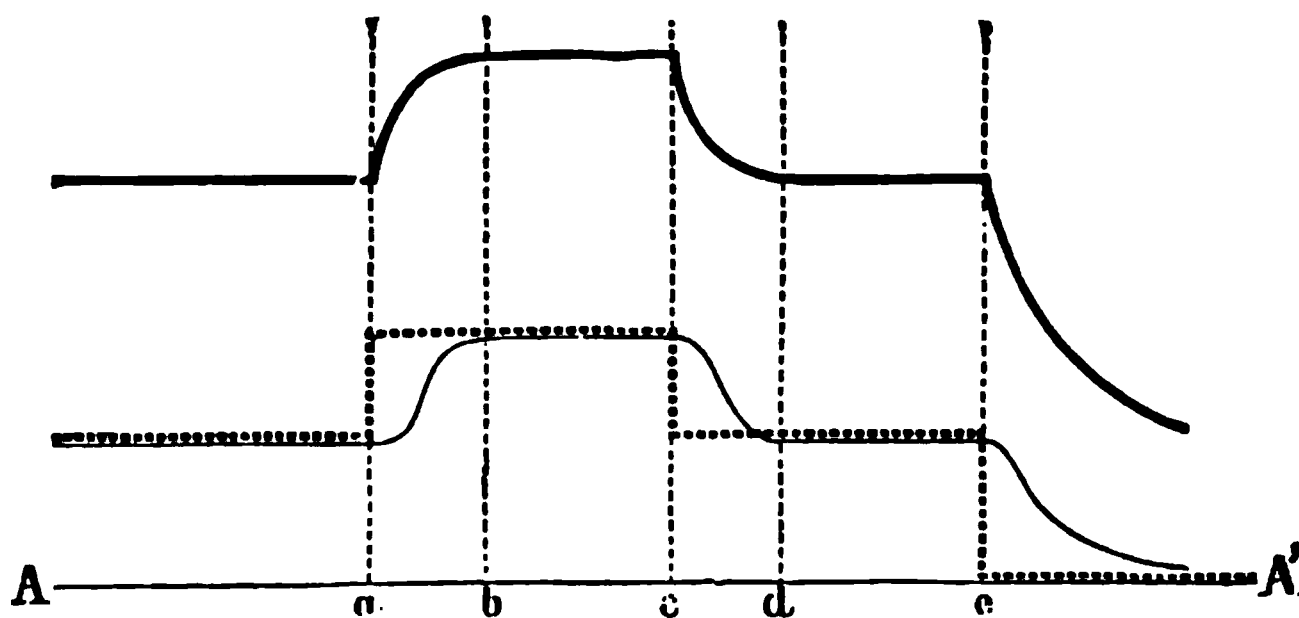
Experience has now taught us that when the body is supplied with an excessive diet, its weight does increase, but that the excretion of oxidized products is also increased, especially the excretion of urea when the diet is highly nitrogenous (C. G. Lehmann, Bidder and Schmidt); further, that if we except the products of the generative organs, unoxidized organic bodies never make their way into the excreta. The second of the above-mentioned hypotheses is, therefore, excluded by the circumstance that the excretions always increase. The third, besides not agreeing with the experimental fact of an increase of weight in over-fed animals, would necessitate a corresponding increase in the amount of oxygen taken into the body, and in the bodily energies or activities, in consequence of the increased extent of oxidation. In a body at rest this increase in the bodily energies could only manifest itself by an increased formation of heat (Chapter VII.) Such an increased formation of heat does, in fact, occur; the augmented digestive activity requiring a greater consumption of material and yielding more heat in the processes of secretion and movement; but the amount is too slight to satisfy the third theory. The

following facts support the fourth of the above methods of disposal.

As in the case of an insufficient allowance of food, so also when the food is administered in excess, the expenditure of the body accommodates itself to a certain extent to the income. This accommodation has been most exactly made out in the case of the albuminous elements (Bischoff, Voit). Whenever an animal is fed for a long time abundantly with albumin, a condition of equilibrium supervenes, after a short time, between the nitrogen in the food and that in the excreta; and this equilibrium is connected with a definite weight of body, which is meanwhile maintained. If the amount of food is suddenly increased, and maintained at the increased rate, the equilibrium is again established, after a certain time, with an increased body-weight. Until this state of equilibrium is reached the excreta are somewhat less than the ingesta, and albumin is stored up in the body, the animal being said 'to make flesh.' If, on the contrary, the amount of albuminous food is diminished, the excreta continue to be somewhat greater than the ingesta in the interval preceding the readjustment of equilibrium with a diminished body-weight; and the animal 'loses flesh.' The organism can, therefore, within certain limits, 'readjust itself' for every alteration in the amount of the food ingested, its constitution undergoing a change. If the amount of food ingested be diminished below a certain point, the condition of hunger supervenes, the laws of which are similar to those above given.

The following figure (fig. 17.) serves to illustrate diagrammatically what has been said. The abscissa-line AA' indicates the time, the ordinates of the thick

FIG. 17.



curve the weight of the body, or its albuminous constituents, those of the thin curve the amount of the daily excreta, and those of the dotted one the amount of the daily ingesta. The ingesta are suddenly increased in amount at a , and at c suddenly diminished, and are at e nothing. aa , bc , de , indicate the periods of equilibrium between ingesta and excreta; ab , the period during which readjustment is in progress when the excreta and the body-weight are both increasing; cd , the period during which readjustment is taking place when the excreta and the body-weight are both diminishing; ea' , the period of hunger,

also characterised by the decrease of both body-weight and excreta. The alterations in the weight of the body on each day are of course determined by the difference between ingesta and excreta.

According to recent investigations (Pettenkofer and Voit), it would seem that a similar relationship between gains, losses, and stock exists in the case of fat as in the case of albumin. The amount of fat stored up in the body is, however, also dependent upon the albuminous ingesta. When, therefore, the latter are increased in amount, there occurs not only an accumulation of albumin, but also of fat. Fat is probably formed during the decomposition of albumin under certain circumstances;—a decomposition occurring which is attended with excretion of urea and retention in the body of certain energy-yielding complex molecules, such as is contemplated in the fourth of the four possible courses mentioned above. What the circumstances are which are favourable to this formation of fat, and whether they are connected with the excessive ingestion of food, cannot yet be exactly stated. On the other hand, the expenditure of albumin is diminished by the simultaneous ingestion of fats or carbo-hydrates, of which fact no explanation has hitherto been given. The very general statement that fats and carbo-hydrates, being easily combustible substances, attract to themselves the oxygen, and in that manner save the albumin, is not very well founded. That the addition of a fatty element to an albuminous diet leads to the accumulation of fat in the body is most probably to be explained by the direct accumulation of the fat ingested, or the diminished use of that already present. On the other hand, the carbo-hydrates of the food are rapidly burned up, and only further the storing up of fat produced at the expense of the albumin or fat of the food, by protecting fat from oxidation; therefore the deposition of fat increases with the supply of albumin, when the quantity of carbo-hydrates remain constant; the converse does not, however, occur, *i.e.* the fat stored does not increase with the carbo-hydrates when the albumin remains constant (Pettenkofer and Voit).

The fats of the body might be derived:—1. From albuminous bodies, as is indicated (*a*) by the appearance of a fatty body (adipocere) in the albuminous tissues of dead bodies; (*b*) by the formation of fat out of casein in standing milk; (*c*) by a similar process in the 'ripening' of cheese; (*d*) by the appearance of stearin in the body, when, in addition to albumin, a kind of fat (palm oil) containing no stearin is taken with the food (Subbotin). Other phenomena which are cited to prove the formation of fat from albuminous bodies, &c., *e.g.* the 'fatty degeneration' of organs rich in nitrogen, cannot be regarded as giving any support to the theory, as they simply show that at one part of the organism, which is in connection with every other part by the continual interchange of material, one body is deposited instead of another, and this cannot, of course, be taken to prove that the one is derived from the other. In like manner, some time since, it was customary to mention among the proofs of the formation of fat from albuminous bodies the fact that the crystalline lens and other nitrogenous bodies destitute of fat when placed in the abdominal cavity of a living mammal became after some time very fatty, having lost some of their nitrogen. But all

the experiments devised to control this result, in which indifferent porous materials, such as wood, elder-pith, &c., were substituted for the fatless nitrogenous body, have shown that these bodies also become impregnated with fat.

2. From carbo-hydrates. Although the transformation of carbo-hydrates into fats would have to be regarded as a process of reduction—unless indeed we suppose the former to yield only the glycerin necessary for the latter—the following circumstances seem to indicate some such operation: (a) Bees fed on sugar alone yield a fatty body, *wax*; (b) Food containing a large quantity of carbo-hydrates tends to fatten the body ('Fattening,' see below), an accumulation of fat taking place immediately, in such cases, in the liver (Tscherinoff). The last-mentioned circumstances admit of another explanation, viz. that the oxidation of the easily combustible carbo-hydrates renders unnecessary the combustion of fat or fat-forming bodies (*e.g.* albuminous bodies); but of this more will be said hereafter. The fact that fats are formed in some fruits (olives) out of carbo-hydrates (mannit) cannot be taken to support the theory that a similar process occurs in animals.

It is now considered that albumin is the only source of the fat in the body, except that which is derived from the fat directly eaten; for in all cases, even in the enormous formation of fat which takes place in milch-cows, the fatty and albuminous materials of the food are sufficient to account for the fat in the milk yielded. Moreover, the production of wax by bees fed entirely on sugar is explicable by the theory of its formation from the albumin stored up; and the fattening of cattle on hydro-carbons is only successful when albuminous food is at the same time taken (Voit, Weiske and Wildt).

Meat can yield to the body about 11 per cent. of its weight of fats (Pettenkofer and Voit). The fat which is derived from a decomposition of the proteids (probably taking place in the tissues) is deposited in the same situation as that directly ingested; it chiefly makes its way into the subcutaneous areolar tissue (Förster). Adipose tissue, especially in the mesentery, is not, according to the results of recent researches (Toldt, Rollett), to be looked upon merely as connective tissue, the cells of which are filled with fat (Virchow), but as a glandular organ with special vessels, and which in man is developed at an early age from connective tissue.

[The view which has been adopted by Professor Hermann concerning the source of fat of the animal body is based upon the experiments of Pettenkofer and Voit¹ and of Weiske and Wildt.² It is, however, in disagreement with the results obtained in a much more extensive but, it appears to the editor, more convincing set of experiments made long ago by Messrs. Lawes and Gilbert,³ to which they have of late again drawn attention.⁴

The question is not whether fat is formed or not at the expense of the proteids of the food, but whether it is ever formed at the expense of the carbo-hydrates contained in it. The experiments of Professors Pettenkofer and Voit showed long ago that when a dog was fed with starch and fat without any proteid, the carbon

¹ Pettenkofer und Voit :—

(1.) 'Ueber die Zersetzungs Vorgänge im Thierkörper bei Fütterung mit Fleisch und Fett.' *Zeitschr. f. Biologie.* Vol. ix. (1873) pp. 1-40.

(2.) 'Ueber die Zersetzungs Vorgänge im Thierkörper bei Fütterung mit Fleisch und Kohlehydraten und Kohlehydraten allein.' *Zeitschr. f. Biol.* Vol. ix. (1873) pp. 435-540.

² Weiske und Wildt, 'Untersuchungen über Fettbildung im Thierkörper, ausgeführt auf der Versuchsstation Proskau.' *Zeitschr. f. Biologie.* Vol. x. (1874) p. 1.

³ J. B. Lawes and J. H. Gilbert, 'On the Composition of Foods in relation to Respiration and the Feeding of Animals.' *Report of the British Association for 1852.*

⁴ J. B. Lawes and J. H. Gilbert, 'On the Formation of Fat in the Animal Body.' *Journal of Anatomy and Physiology.* Vol. xi. (1877) pp. 577-588.

stored up could all be accounted for as derived from the fat present in the food plus that derived from the transformation of the proteids of the body. By increasing the starch the amount of carbon stored up was decreased, presumably because the starch protected the proteids from oxidation and limited the formation of fat. In the dog there was no evidence, at any rate under the conditions of Pettenkofer and Voit's experiments, that any formation of fat from starch or sugar ever took place.

In experiments made upon ruminants, Messrs. Lawes and Gilbert also found that no data could be obtained, which directly proved that in them fat is formed directly from starch or sugar. In these animals, however fed, 'owing to the comparatively small amount of increase obtained with them from a given amount of constituents consumed, the quantity of nitrogenous substance passed through the system for the production of a given amount of increase is, in most, if not in all cases, so large as, in the absence of proof to the contrary, to admit of the assumption that the whole of the fat formed had its source in transformed nitrogenous tissue. At any rate, no absolute proof of the derivation of fat from the carbo-hydrates can be obtained from data of the kind in question relating to such animals.'

The pig, however, as experience had long taught, and as Lawes and Gilbert have shown, is an animal which possesses in a remarkable manner the power of utilizing the food which it consumes, and in which it can be demonstrated that fat is formed at the expense of the carbo-hydrates of the food. In proportion to a given live-weight, the pig consumes a very much larger quantity of dry food within a given time than either oxen or sheep; it gives several times as much increase in relation to a given live-weight within a given time, much more increase in relation to a given quantity of dry food, and a larger proportion of fat in that increase. Further, as Messrs. Lawes and Gilbert state, the most appropriate fattening food of the pig contains a larger proportion of readily digestible carbo-hydrates than that of ruminants.

In the very numerous experiments of Lawes and Gilbert (which contrast remarkably in this respect with those of Wieske and Wildt) the food in different experiments was varied as to the proportion of nitrogenous constituents to carbo-hydrates, and in many cases the animal was allowed to fix its own diet. It was conclusively proved that 'when the proportion of the nitrogenous to the non-nitrogenous substances in the food was the most appropriate for fattening, there was a much larger proportion (about 40 per cent.) of the total produced fat which could not possibly have had its source in the nitrogenous substance consumed.' Not only did the amount of increase in live-weight bear a relation to the amount of nitrogenous substance supplied, but the more

excessive the supply of it the greater was the tendency to grow and the less the tendency to fatten.

It is nearly certain that all further experiments will confirm the very extensive and thorough researches of Lawes and Gilbert, and prove that the fat of the body is derived from all the chief groups of organic constituents of the food, viz., from the fats, from the carbo-hydrates, and from the proteids.]

The increased consumption of proteids which takes place when their supply is increased (Pettenkofer and Voit, contradicted, however by Speck) is associated with an increase in the consumption of oxygen, the decomposition which occurs being one depending upon oxidation.

If the amount of albumin burned be calculated from the amount of nitrogen excreted, it is found that all the carbon does not make its way into the excreta, proving that a substance richer in carbon (fat, glycogen) is produced by decomposition and retained (Pettenkofer and Voit).

It is disputed whether the decomposition of albumin which takes place in consequence of an increased supply occurs at the expense of the newly ingested or of the old and already organized proteids, the consumption of which would then be regulated in an inconceivable manner by the supplies of new albumin. A direct consumption of substances taken in excess—which used formerly to be designated “luxus consumption”—might occur in the blood itself or in the tissues; the second supposition appears the more likely, as hitherto no processes of oxidation have been with certainty determined to take place in the blood itself; according to this hypothesis it would be that part of the ‘circulating’ albumin which has not yet been deposited in the tissues which would be decomposed; the ‘albumin of organs’ would, however, remain intact, *i.e.* would be decomposed during the work of organs (Voit). A direct proof of this is afforded by the fact that transfused blood, which may be looked upon as a superadded tissue, scarcely increases the amount of urea excreted in a perceptible manner, whilst transfused serum or blood ingested as food does increase it (Tschiriew, Forster).

Lately, the profound decomposition (into leucine, tyrosine, &c.) which the proteids undergo in the intestine has been looked upon as a ‘luxus-consumption;’ many considering peptones as a part of the ingested proteids destined for direct combustion. [The experiments of Plosz and Maly, referred to on page 50, directly contradict this.]

The consumption of proteids is, leaving aside the influence of the supply of albumin, of fats, and carbo-hydrates, influenced to a certain extent even by the amount of the salts consumed. A moderate consumption of common salt has been stated to exercise a moderating influence upon the consumption of albumin (Klein and Verson,¹ contradicted by Forster²), whilst a large consumption of common

¹ Klein u. Verson, *Sitzungsber. d. k. k. Akadem. d. Wissensch. zu Wien*. 1867, p. 627.

² Forster, ‘Versuche über die Bedeutung der Asche-bestandtheile in der Nahrung.’ *Zeitschr. f. Biol.* Vol. ix. (1873), pp. 297–380.

salt exerts the opposite influence (Voit). (Common salt appears especially to exert a favourable influence in the case of herbivorous animals, Bunge.¹) Even the amount of water ingested has an influence, abundant drinking increasing the amount of urea excreted—a result which must be referred to decomposition of albumin, seeing that physical conditions could not continuously increase the amount of urea.

Whether the supply of oxygen influences the decomposition is disputed. The statement that even the activity of the respiratory movements influences the processes of oxidation, as measured by the gaseous interchanges, has been shown by recent researches to be incorrect, as the amount of oxygen taken up in apnoea is not increased (Pflüger with Finkler and Oertmann). A continuously diminished supply of oxygen, which was formerly supposed to diminish decomposition, or at least to lead to the excretion of unoxidized matters (as sugar, &c.), not only does not diminish the decomposition of albumin decomposed (Senator), but actually increases it (Fränkel), a fact which has not yet been fully elucidated.

The degree of functional activity of the organism has a great influence upon the magnitude of the exchanges of the body; even light increases them, doubtless through nervous stimulation (Moleschott, Pflüger and v. Platen); in sleep they are perceptibly diminished (Pettenkofer and Voit); but muscular work influences them specially.

The temperature of the tissues bears a direct relation to the rate of decomposition going on within them; when cold-blooded animals are exposed to heat, the consumption of oxygen and the production of carbonic acid are increased (Moleschott, Regnault and Reiset, Pflüger and Schultz). The same result occurs even in warm-blooded animals if their temperature be artificially altered (Ludwig and Sanders-Ezn, Erler), increase in the urea excreted being also produced (Schleich). Within the limits of constant temperature, however, the opposite, according to some observers, appears to be the case; an increase in the rate of decomposition being brought about by cold and a diminution by heat through the intermediation of nervous apparatus (Vierordt, Letellier, Pflüger and Colosanti).

As a result of the varying intensity of functions, the process of decomposition as shown by the carbonic acid and urea-excretion, exhibits a diurnal curve, which is parallel to the curves of temperature, pulse and respiration: this curve exhibits in general a minimum in the night or towards morning, and a maximum in the afternoon or evening: meals lead to superposed fluctuations.

In hibernating animals which may fast for months, both processes of decomposition and bodily activity are lowered to a minimum (compare Chap. VII.) In frogs the respiratory exchanges at 1° C. well nigh approach zero, whilst at 36° they become equal to those of warm-blooded animals (Pflüger).

¹ Bunge, 'Ueber die Bedeutung des Kochsalzes und das Verhalten der Kalisalze im menschlichen Organismus.' *Zeitschr. f. Biol.* Vol. ix. (1873), pp. 104–143.

PART II.

THE ACTIVITIES OR ENERGIES OF THE BODY.

INTRODUCTION.

IN the general Introduction to this work it is stated that the animal body is the seat of transformations of potential into kinetic energy.

It may be stated generally that the potential energy of the body is associated with two kinds of matter, widely separated from one another, viz. atmospheric oxygen on the one hand, and the oxidizable constituents of the body, which enter it as food, on the other. Energy-yielding substances are, therefore, being continuously introduced into the body. It has, further, already been stated, that the products of the combination of the above-mentioned different kinds of matter, *i.e.* oxidation-products, are continually being thrown out of the body.

Similarly, it has now to be stated that the energy which has become kinetic in the animal body is continually being transferred from it to bodies existing in the medium outside and independent of it. Just as, however, the expenditure of the matter of the body is always a little below its income (and this difference is necessary to the existence and persistence of the body), so also the expenditure of energy is always below its income, for the organism always contains a certain store of energy, part of which is potential in its yet unoxidized constituents, part of which is kinetic—its heat.

The transformations of the energy of the body run side by side with the exchanges of its matter. As in the preceding chapter, the gains and losses of the matter of the body have been discussed and compared, the same task must now be undertaken in reference to its energies, whilst these must, as far as possible, be brought into relation with the exchanges of matter. The scanty knowledge yet possessed on this subject merely permits of the discussion of some of its salient points.

Introduction of Potential Energy into the Body.

Although the potential energy which has here to be considered is associated, not only with the matters to be oxidized, but also with oxygen, we usually only speak of the energy of the alimentary substances of the food, whilst we tacitly and correctly assume the presence of the quantity of oxygen required to oxidize them. The potential energy of the oxidizable (organic) alimentary constituents is usually expressed as heat, *i.e.* the total kinetic energy which can be developed by the oxidation is represented as heat, although, as can be proved, forms of energy other than heat arise from them.

This simplification possesses great advantages for quantitative determinations.

The determination of the heats of combustion of the alimentary substances is easily effected by burning them in a calorimeter, *i.e.* a chamber surrounded on all sides by some liquid, generally water. The temperature of the liquid, the amount of which is known, is determined before and after the combustion. The result, which is the amount of heat produced, is expressed in 'units of heat' (see page 5), and furnishes a measure of the heat of combustion. The difficulties which attend this experimental determination are, however, great in the case of many of the alimentary substances, so that the heat of combustion of many is not accurately known.

Although, in the animal body, the combustion of the alimentary substances (or of the constituents of the body which originate from them) does not take place suddenly, as is the case in artificial combustion, but gradually, yet the results of calorimetrical determinations do afford a measure of the heat developed in the slower oxidations; *for the sum of all the heats developed in the individual successive oxidations, or decompositions of any other kind, which a body undergoes before it is completely burned (so as to yield carbonic acid, water, sulphuric acid, &c.) is equal to the heat which is directly developed by perfect combustion.*

A method of very simply determining the heats of combustion which has been adopted by some scientific men is not trustworthy, and leads to false results. They have, namely, attempted to calculate the heat of combustion of a compound from the known heats of combustion of its elements; to do this they suppose the oxygen which exists in the compound itself to be already combined, partly with hydrogen or carbon; it appears, however, firstly, that the bases for such a hypothesis are wanting; and secondly, that the other elements of a compound are bound together with a certain amount of energy, so that to separate them one from the other, a portion of the kinetic energy developed in the combustion must be consumed: the results obtained by such a method must therefore differ from the results of direct experiment by an amount which corresponds to the energy used up in the dissociation process just referred to.

In the case of chemical compounds of *known constitution* (and few of the

alimentary substances can as yet be classed under this category) the heats of combustion can be calculated according to simple rules. A sufficiently close approximation may be obtained for 1 gramme of substance, by giving to each C-C-combination in the molecule, the value $a = 37,000$ heat units; similarly to each C-H-combination, the value $b = 55,000$ heat units; to each C-N-combination, the value $c = 39,000$ heat units; and to each N-H-combination, the value $d = 10,000$ heat units; adding up all these values and dividing the sum total by the molecular weight of the substance (Hermann). Thus, e.g. the heat of combustion of glycine (p. 39)

$$= \frac{a + 2b + c + 2d}{75} = 2747 \text{ heat units.}$$

In the case of more accurate calculations, other corrections have to be introduced (Hermann).

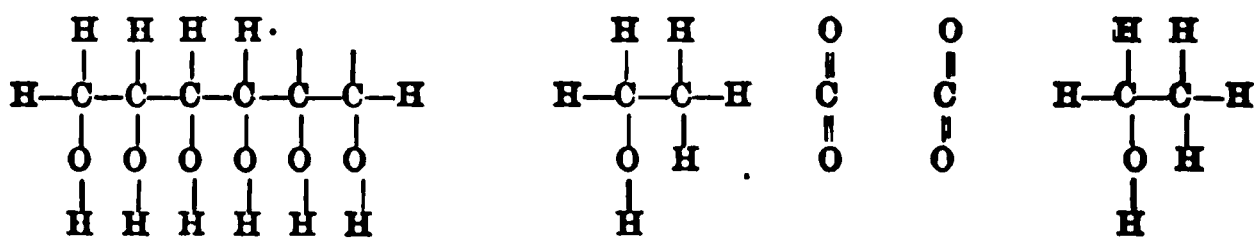
From experimental determinations it has been made out that in complete combustion 1 gramme of albumin generates 4998 heat units, 1 gramme of beef (freed from fat) 5103 heat units, 1 gramme of beef fat 9069 heat units. When oxidized so as to yield urea, albumin is calculated to furnish 4263, and beef 4368 units of heat (Frankland). By calculation it is found that 1 gramme of stearin develops 9036, 1 gramme of palmitin 8883, 1 gramme of olein 8058, 1 gramme of glycerin 4179, 1 gramme of leucine 6141, and 1 gramme of creatine 4118 units of heat (Hermann).

Origin of the Kinetic Energy of the Body.

(The Energies of the Body.)

Oxidation (as has already been repeatedly stated) is the process which, far more frequently than all others, leads to the transformation of potential into kinetic energy. We cannot, nevertheless, forget that oxidation is not the only process associated with the liberation of energy, but that it is only one of the processes, though certainly by far the most frequent, which prove the general law that *in every chemical process, in which stronger affinities are saturated than were saturated before its occurrence, potential energy becomes kinetic.*

An example of a process not dependent upon oxidation in which, however, heat is generated, is afforded by the alcoholic fermentation of sugar.



As the above graphic formulæ indicate, carbon atoms, which in sugar are linked either to carbon or hydrogen atoms, are, after the decomposition, linked to oxygen atoms. As, however, the attraction of carbon for oxygen is greater than it is for carbon or for hydrogen, this change in the position of atoms must be associated with the liberation of energy. As these groups of atoms which result from such a process of decomposition are bound together by stronger affinities than those which existed before, the new compounds are more stable;

and it may be stated as a general proposition that in operations attended by the formation of chemical compounds, or of more stable compounds than existed before, potential energy becomes kinetic. Under this general law are included the ordinary processes of oxidation, as well as others which are analogous to the fermentation of sugar.

The forms of energy in which the kinetic energy developed in the body from the potential energy introduced into it may manifest itself are, so far as we know, heat, electricity, and mechanical work. When the animal body is in a state of rest, viz. when all kinds of work which are not absolutely essential to the continuance of life are avoided, it may be stated that all these forms of energy are almost entirely transformed into a single form—heat.

The form which energy (see the Introduction) may assume is, as we know, very variable; heat is easily converted into motion (as in the steam-engine), motion into heat (by friction); both heat and motion into electricity (frictional- and thermo-electricity); and electricity into heat (as evidenced in the heating of wires along which a current of electricity is passing) and into motion (electro-magnetism).

Nevertheless the amount of kinetic energy always remains constant, though such transformations occur, for they always proceed in definite proportions (equivalents). The most important of these equivalents is the 'Mechanical Equivalent of Heat,' i.e. the mechanical work into which a certain amount of heat may be converted, or conversely (see p. 4).

The *formation of heat* goes on directly in all organs of the body in which processes of oxidation occur, i.e. in all, except the horny, tissues.

Electricity, so far as we yet know, is only developed in the muscular and nervous systems (Chapters VIII. and IX.)

Movements occur with perceptible rapidity, 1. in the striped and smooth muscular fibres; 2. in contractile cells; 3. in ciliated cells; 4. in spermatozoids; whilst other movements take place with such slowness in all organic forms that they cannot be perceived; such occur during growth, in the fission of cells, &c.

The evolution of light (phosphorescence) has been observed to occur in many animals, sometimes over the whole surface, sometimes in connection with the individual organs, which are internally associated with the respiratory apparatus. The phosphorescence of decomposing fish, of decomposing wood, &c., depends upon the presence of minute organisms, and is connected with the access of oxygen (Pflüger).

The proof that, in the body when in a state of rest, all forms of energy are converted into heat, and are in this form transferred from it to the external world, rests upon the following facts:

1. Movements which occur in the body when at rest do not, as such, exert any action upon the medium outside of it, but disappear within the body itself. This disappearance is brought about chiefly by *friction*: thus, the whole of the kinetic energy of a cardiac contraction expended on the mass of the blood imparts to it *motion*; in the course of the circulation this motion, by fric-

tion against the walls of the blood vessels, and especially of the capillaries, ceases to exist. This same disappearance of motion is observed in the case of alimentary apparatus, where it occurs partly in consequence of friction against the contents and against the structures which surround it.

As no other mode of motion (*e.g.* electricity) is known to result from this friction, we are led to suppose that, everywhere, a quantity of heat is generated which is equivalent to the motion, *i.e.* mechanical work, which disappears.

2. Even the small quantities of electricity developed in the nervous and muscular systems appear, in great part, to be converted into heat (Chapter VIII.)

Exceptions which, judged of quantitatively, are of very small importance must be made to the general statement previously enunciated, that in the body at rest, the only form of kinetic energy imparted to the medium around it is heat: thus, (1) the movements of respiration, of the heart, of the pulse may be communicated to bodies outside the organism; and (2) electric currents may be conducted away from the surface of the body to surrounding objects by the interposition of conducting media (Chapter VIII.)

In the animal body when at work there originates an increased quantity of kinetic energy, in addition to that which is being produced during rest. This energy, which is developed within the muscles, takes the form of heat and mechanical work. Of this mechanical work a great part is converted, within the organism itself, into heat by the friction of the muscles and tendons within their sheaths, and by the movement of bones in their articulations. The remainder of the mechanical work is employed, partly in effecting the movement of the various parts of the body in reference to one another, partly in moving the body as a whole through the medium which it inhabits, and partly in effecting the movements of bodies which exist in that medium.

Seeing that even the last-named portion of the energy of the organism (*viz.* that expended on the bodies of the external world) is easily converted into heat, and may be expressed in *units of heat*, it is evident that the natural measure of the whole of the energies of the body is the amount of heat corresponding to them.

One might, naturally, just as well express the whole energy according to its mechanical equivalent, *i.e.* in units of work instead of units of heat (as kilogrammetres, foot-pounds, &c.)

The numbers of heat units which express the kinetic energy of the organism are enormously great, amounting to several millions per diem. Some employ in their calculations an unit of heat which is a thousand times greater than that usually employed, defining the unit of heat to be that quantity of heat which will raise one *kilogramme* of water from 0° C. to 1° C.; the mechanical equivalent of this unit is then = 424 kilogrammetres.

Expenditure of Energy.

With the exception of the small quantity of energy which the organism loses in its imperfectly oxidized organic excreta (urea, uric acid, milk, &c.), all the potential energy of its food passes as kinetic energy to the outer world. From what has been previously stated, this energy escapes from the body at rest only in the form of heat, whilst in the case of the body which is doing external work in the form of heat and mechanical work. The modes in which heat is given out to the bodies of the outer world will be treated of in the following chapter; the transfer of mechanical work needs no further discussion.

The direct measurement of this expenditure of energy (heat) is effected, in the case of the body at rest, by placing the man or the animal, exactly as a burning body, into a calorimetric chamber adapted to the purpose. In the case of the body engaged in performing external work an arrangement is provided within the chamber which permits of the work done being measured; such, for example, as a treadmill which is connected with a steam-engine, and which the man under observation ascends or descends, so as to perform an amount of work (either in accelerating or retarding the movement of the wheel) which permits of being estimated (Hirn). From the quantity of mechanical work thus estimated the equivalent number of units of heat may be calculated and added to the expenditure of heat as found by the direct method.

(For the magnitude of the expenditure of heat and of the mechanical work done, as well as for their relations, consult the two following chapters.)

Comparison between the Gains and Losses of Energy.

The object of attempting a comparison between the energy which enters and leaves the body is, firstly, to confirm the theoretical conceptions which we have formed, and secondly, to check the separate determinations of gains and losses.

As has been previously mentioned, the amount of energy received into the body can be determined if we know the amount of the organic constituents of the food and the heat which they develop on combustion; and at the same time it has been stated that for only a few of the alimentary substances has this heat of combustion been accurately determined. We must therefore rest satisfied with estimating the kinetic energy corresponding in a given time to the potential energy at the disposal of the body, and comparing it with the actual amount of energy given out.

The former of these data is estimated according to the following principle: every manifestation of energy is necessarily

associated with a corresponding consumption of oxygen, and the consumption of oxygen is, if estimated for long periods of time, equal to the oxygen received into the body. From the oxygen received we might calculate the amount of energy which becomes kinetic, if the whole of the oxygen were used up in the oxidation of one and the same body, whose heat of combustion were exactly known.

Since different compounds of unequal heats of combustion are oxidized, the knowledge of the amount of oxygen received cannot be utilized. But from the oxidation-products which are excreted in a given time we can, at any rate approximately, determine the elements which are oxidized, as, for instance, the carbon from the carbonic acid, and the hydrogen from the water, produced in the course of oxidation. The amount of water which is formed in the body can, however, scarcely be estimated, and we are therefore compelled to subtract the amount of oxygen which corresponds to the carbon (*i.e.* required to oxidize the carbon to form CO_2), and assume that all the remaining oxygen is employed in the oxidation of hydrogen. The error doubtless arising from this dogmatic assumption becomes insignificant when compared with the much larger one, due to our determining the heat of combustion of the carbon and hydrogen found, as equal to the heat which is developed by the combustion of their organic combinations.

As we should expect from these considerations, such researches (as those of Dulong and Despretz) have led to no agreement between the expenditure of heat as calculated and as directly measured.

An attempt has been made to determine, in the case of the energy of the body as in that of its matter, by what channels its distribution is effected. The numbers which have been obtained by calculation, being affected by numerous errors, which have in part been already mentioned, need not be quoted; the results of these calculations possess therefore only the value which attaches to an approximate estimate. According to Barral's calculations the expenditure of the energy of the body is distributed as follows: from 1 to 2 per cent. is lost in heating the excreta (urine and fæces), 4 to 8 per cent. is lost as heat in the respiratory processes, from 20 to 30 per cent. is used up in the evaporation of water; the greatest part (60 to 75 per cent.) leaves the body either as heat conducted or radiated from its surface, or is converted into external mechanical work. (Concerning the importance of this question consult the succeeding section.)

Influence of the Conversion of Energy on the Exchanges of Matter.

In the preceding chapter it has been shortly stated that the oxidation-processes of the body must necessarily reach a certain amount in order that the organism may continue to exist, and that this amount constitutes the 'minimum exchange of its matter.' A closer investigation into the causes which render this minimum exchange necessary reveals at once that the necessary oxidation-processes are required for the supply of the energies of the body, viz. for the development of heat, for the performance of certain kinds of mechanical work (as for the movement of the heart, the movements of respiration, of the alimentary canal, &c.) Occasionally certain processes are required for the sake of their products (*e.g.* characteristic products of secretion).

It has already been mentioned that when the chemical transformations of the body are increased by diet in excess of the bodily requirements, the activities of the body are also increased. The case remains to be considered in which, through an increased activity of the body, an increase of the matter received by the body is necessary. This increased receipt of matter has been termed by German writers 'Arbeits-Consumption,' *i.e.* the diet which the body requires to enable it to do work.

We know by experience that the mechanical work of the muscles, which we shortly designate *work*, is that act of the body associated with transformation of energy, which is most frequently, and to the greatest extent, influenced by the will, by reflex action, by cramps or convulsions due to disease, &c. An increase in the amount of this work is associated with increased exchanges of matter, and consequently leads to an increase in the excretions, especially to an increased excretion of carbonic acid, and necessitates, if the weight of the body is to remain constant, an increased consumption of food ('Arbeits-Consumption'); at the same time, the sensation which indicates the want of food, viz. hunger, is increased.

It is yet disputed whether, under certain circumstances, especially as a consequence of losses of heat, an increased production of heat takes place in the body, quite independently of muscular movements, but in accordance with certain fixed laws. On this subject the reader must consult the following chapter.

As will afterwards be stated in detail, the different manifestations of energy in the body are associated with the consumption of specific constituents. In order to form a judgment as to the article of diet which would best supply the increased consumption due to any given act, we should require to know the constituent

which is principally consumed during that act. The most direct way to acquire this knowledge would appear to be to study the separate organs, as *e.g.* the muscles, in which the various manifestations of energy are observed, and in which the chemical changes proceed. As, however, this department of physiology is yet but little developed, we must satisfy ourselves with a study of the changes in the excretions, which correspond to increased evolution of kinetic energy. Especially the amount of urea has to be studied as evidence of the oxidation of nitrogenous bodies, and the amount of carbonic acid as expressing the oxidation-processes of the body in general.

In consequence of doubtful statements (especially one which asserted that muscular activity increased the excretion of urea) the view was, for a long time, promulgated that only those nitrogenous constituents of the body which enter into the composition of the tissues are made use of in the production of mechanical work. It was supposed that no heat was developed from these nitrogenous constituents until by processes of decomposition they had furnished non-nitrogenous substances. The non-nitrogenous constituents, on the other hand, were supposed to be simply employed in the production of heat.

Upon these hypotheses was based a classification of foods, according to their uses. The nitrogenous constituents were, because of their relation to the tissues, called 'plastic' (or 'flesh-formers'); the non-nitrogenous, on the other hand, were called 'respiratory' constituents; or, the former were designated as the sole generators of movements, 'dynamogenous,' or 'kinesogenous,' while the latter, as the sole generators of heat, were spoken of as 'thermogenous' (Bischoff and Voit). Since it has been ascertained, however, that the excretion of urea is not increased during mechanical work, this hypothesis has fallen to the ground; and the importance of the numerous considerations opposed to it is now fully recognised. Among these the following must be mentioned (M. Traube): 1. That even with a food which is very poor in nitrogen (vegetable food) a considerable amount of mechanical work can be performed (the majority of beasts of burden are herbivorous, and bees, though fed merely on honey, are continually in motion). Such facts as these could only be brought into harmony with the old theory, by supposing that the mechanical work of the body, even when it attains a high magnitude, is insignificant in amount when compared to the heat formed—a view which has already been combated. 2. That cold-blooded animals, and even animals and men inhabiting hot zones, and whose heat-production can only be very small, yet live, in great part, on a vegetable diet containing but little nitrogen. 3. That carnivorous animals, in spite of the small quantity of non-nitrogenous food which they consume, have sufficient heat generated within them, even when they do not perform

much mechanical work. 4. It has lastly been directly ascertained that the albuminous bodies which are consumed in a given time (calculated from the amount of urea excreted) are not by any means capable of accounting for the work done during the same time, even though the heat of combustion of those bodies was calculated extravagantly high (Fick and Wislicenus). Moreover, the inhabitants of mountainous districts prefer to take bacon and sugar as provisions when they have arduous journeys to perform.

We cannot, therefore, point to any act accompanied with the evolution of kinetic energy, for which the consumption of a particular kind of food (nitrogenous food) is absolutely necessary.

CHAPTER VII.

ON THE DEVELOPMENT OF THE HEAT AND ON THE TEMPERATURE OF THE BODY.

I. DEVELOPMENT OF HEAT.

BUT little remains to be said concerning the origin of the heat of the animal body. It has been repeatedly stated, that in all organs in which processes of oxidation occur, either the whole of the energy which becomes kinetic, or, at least, a considerable fraction of it, takes the form of heat. The other forms of energy (mechanical work, electricity) are only generated in certain organs, and then only in addition to heat.

According to recent investigations even the lungs belong to the group of heat-generating organs; in the lungs the combination of oxygen with hæmoglobin is a source of heat.

The absolute amount of heat generated in the unit of time, by the unit of weight of any organ, is as yet undetermined; it varies greatly, however, in the case of different organs. The glands, for example, generate far more heat than the parenchymatous tissues, because the oxidation-products of the former (the specific constituents of the secretion) are continually being removed and replaced by newly formed substances. The oxidation-products of the latter, on the other hand, *i.e.* the specific constituents of the parenchymatous juices, remain very long in the place where they originate; oxidation is therefore far more active in glands. Even in one and the same organ the development of heat varies very materially at different times, and, as is readily conceivable, with the energy of the oxidation-processes, or, which is the same thing, with the amount of oxygen which is consumed.

The increased generation of heat dependent on the energy of the oxidation-processes is particularly remarkable in the case of glands, the temperature of which notably increases as the secretion becomes more active. Even in muscles an increased development of heat is observed during activity. (Consult the following chapter.)

No heat is generated in the horny tissues of the body, in which, it would appear, no oxidation-processes occur. Whether heat is generated in the blood can only be determined by answering the question as to whether oxidation goes on in that fluid.

In addition to the direct sources of heat which have just been referred to, there are also others which have been previously treated of. It has, namely, been ascertained that in the body when it is at rest, other forms of kinetic energy, particularly mechanical work, are almost entirely converted into heat. This conversion into heat occurs partly through the friction of the actively moving organs (muscles) against the tissues with which they are in contact, and partly by the friction and dragging of passive organs (tendons, bones, blood in the vessels, &c.) brought about by those which are in active motion. Thus, in the body which is doing work, a great part of the mechanical work is, by friction, converted into heat.

Muscular work consequently increases the production of heat in the body, in a twofold manner: 1. By increasing that production of heat in muscle which is connected with muscular activity. 2. By the friction of the muscle and of the structures moved by it against the surrounding parts.

It is yet undecided whether the production of heat in the parenchymatous tissues (considered apart from glands and muscles) is directly under the control of special nerves. The majority of the changes in temperature which follow the section or the irritation of nerves can be explained by the influence exerted upon the distribution of heat through the vaso-motor nerves (see below). Still, some recent observations appear to point to a direct influence exerted by the nervous system upon the production of heat.

Under certain circumstances, after traumatic lesions which interrupt the continuity of the spinal cord, or after its division (Brodie,¹ Billroth, Quincke), a rise in the temperature of the body occurs. Seeing that division of the spinal cord would by its influence on the vaso-motor nerves cause a lowering of the temperature, the rise which occurs under such circumstances has led to the supposition that certain fibres exist in the spinal cord which have a direct influence on the production of heat, being capable of inhibiting it. The inhibitory centre presiding over these nerves would, according to this theory, have to be sought for in the brain (Naunyn and Quincke²). In order that rise in temperature may occur after division of the spinal cord, the counterbalancing influence exerted by the vaso-motor nerves must be prevented, by hindering the external loss of heat. Some have failed to observe any rise of temperature as a consequence of division of the cord (Rosenthal).

Even when the medulla oblongata is separated from the pons Varolii, and when both the portions of the brain are injured, rises in temperature occur (Tscheschichin; Bruck and Günther; Schreiber) which cannot yet be adequately explained.

¹ Brodie, *Physiological Researches*.

² Naunyn u. Quincke, *Archiv. f. Anat. u. Phys.* 1869, pp. 174, 521.

II. TEMPERATURE OF THE BODY.

The different organs of the animal body are in relation with one another, in part by actual contact, and in part through the circulating blood, which acts as a conductor or distributor of heat. Through its agency, the heat generated in the different parts of the economy is distributed pretty uniformly throughout the body, and even to those parts of it which do not themselves generate heat. The result of this equalisation, as well as of the losses of heat about to be discussed, is an approximately constant temperature of the whole body, which in the human subject varies between 36°C . and 38°C . The temperature is nearly the same in other mammals; it is higher in birds. Organisms which possess a constant temperature are called *warm-blooded* or *homo-thermous*. In other animals the energy of the oxidation-processes, and consequently the heat generated, is so small in amount, that there is no constant body-temperature, which merely rises a few degrees above that of the surrounding medium (air or water). Such animals are called *cold-blooded*, or, more appropriately, *poikilo-thermous* (of variable temperature).

Sources of Loss of Heat.

The animal body, being almost always surrounded by media which are colder than itself, is constantly giving out heat to them. This loss of heat occurs in the following manners: 1. *By radiation* from the free surface of the body. 2. *By conduction*. a. To those bodies which are in contact with the surface and are colder than the body, especially air and clothing. b. To the bodies taken into the organism, air and food, which are colder than it. The last-named loss of heat is frequently expressed by saying, that the body gives up heat with its excreta (expired air, sweat, urine, fæces), which possess, in general, the temperature of the body. Obviously these are two ways of expressing the same facts, assuming, as is generally the case, that the matters taken into and excreted from the body are equal in quantity and possess the same specific heat. c. To excreta, especially sweat, which have to be evaporated, and which, during evaporation, remain in contact with the surface of the body; the heat thus given up becomes forthwith latent. It is usual to express this loss of heat as 'heat lost by the evaporation of water.'

As the loss of heat takes place principally from the surface of the body, its amount depends upon the extent of that surface; and it is therefore clear that small individuals, the external surface of whose body, as compared with their body-weight, is more extensive, give up relatively more heat to the medium which surrounds them than do larger ones.

Many of the losses of heat here referred to are of very variable nature; and their variability is utilized in maintaining the constancy of the temperature of the body.

Local Temperatures.

For reasons which are easily intelligible, the above-mentioned equalisation between the temperatures of the different parts of the body cannot be complete, so that certain differences in temperature constantly exist. These differences, which, without any further explanation, may be surmised from the relations of the body already alluded to, have by experiment been fully determined to exist; they are principally the following: 1. The greater the amount of heat which any part of the body generates, the warmer it is (*cæteris paribus*). Glands are, therefore, hottest during secretion, and muscles during work (and during *rigor mortis*); the horny (epithelial) tissues are the coldest. 2. The greater the amount of heat which any organ must lose by radiation or conduction, in consequence of its situation or of other relations, the colder it is. Hence the following structures are the coolest: the skin, particularly when it is covered with sweat; the lungs; the first portions of the alimentary canal; &c. 3. Amongst these parts of the body, those are coldest which are most exposed, those warmest which are most protected (*e.g.* the axilla, the cavity of the mouth, &c.) As the blood is the most important agent in the equalisation of the temperature of the different parts of the body, its temperature might be taken as representing the mean temperature of the body; as a fact, the numbers which have been given at page 256 are deduced from observations of the heat of the blood. From the facts stated we may further conclude: *a.* In organs which generate much heat, and whose temperature therefore exceeds that of the blood (glands, muscles during work), the venous blood which flows out of them is warmer than the arterial blood which flows into them; the opposite is the case with organs which produce little heat, or which give up heat to the external medium; thus, for example, the venous blood of the skin is cooler than the arterial. According to some observers (Colin,¹ Jacobson and Bernhardt²), the heat which the blood in the lungs loses to the air is more than compensated for by the combination with oxygen, so that the blood of the pulmonary veins and of the left side of the heart is hotter than that of the right side of the heart. According to others, however (G. Liebig,³ Bernard,⁴ Heidenhain and

¹ Colin, *Annales des Sciences Naturelles*. 3rd series, vol. vii. (1867), p. 83.

² Jacobson u. Bernhardt, *Centralblatt f. d. med. Wissensch.* 1868, p. 643. *Virchow's Arch.* Vol. li. p. 1.

³ G. Liebig, *Ueber die Temperatur-unterschiede des venösen und arteriellen Blutes*. Giessen, 1853.

⁴ Bernard, *Comptes Rendus*. Vol. xliii. (Aug. 18, 1856). *Leçons sur les propriétés physiologiques des liquides de l'organisme*. Vol. ii. p. 63 et seq.

Körner¹), the opposite is the case; a fact to be explained, according to Körner, not by the small losses of heat sustained in the lungs, but by the fact of the thin-walled-right side of the heart lying near the warm abdominal viscera in its vicinity. *b.* An organ whose temperature is below that of the blood becomes warmer in proportion as the amount of blood flowing into it in the unit of time increases. The temperature of such organs (as the skin) increases under the following circumstances:—when the blood-pressure of the whole body is raised; when the activity of the heart is increased; and particularly when the arteries supplying them are dilated (as when their vaso-motor nerves are divided). On the other hand, under opposite circumstances, the temperature falls. Hence, redness of any portion of the skin is, as a rule, accompanied by heat, paleness by cold.

Even the heat of inflamed parts merely depends upon a more active supply of blood to them, and not upon an increased local production of heat, as it is constantly lower than the normal temperature of the internal organs (Hunter, Jacobson and Bernhardt, Schneider).

These relations must always be kept in mind in determinations of the temperature of the body as a whole. As it is only in the case of the lower animals that the temperature of the blood can be directly determined by placing thermometers in the vessels, in man those parts are chosen for observation of temperature which are least exposed to loss of heat; the thermometer is therefore placed in the cavity of the mouth, in the rectum, in the vagina, or in the axilla, and is allowed to remain there as long as possible. It must here be mentioned that a high temperature of the external zone of the body, by increasing the loss of heat, leads to a cooling of the interior. Conclusions cannot, therefore, be safely drawn from determinations of the temperature of the external zone as to the temperature of the interior of the body; the latter can be determined by placing the thermometer deeply into the rectum. Absolute determinations of temperature are always made with the (mercurial) thermometer. Comparisons of the temperature of two parts of the body, or of the temperature of the same parts at different times and under different conditions, &c., are conducted either with the aid of the thermometer, or better still, by thermo-electric methods (Chapter VIII.)

Maintenance of the Mean Temperature in Warm-blooded Animals.

The mean temperature which has been stated to exist in man and warm-blooded animals appears to be an absolutely necessary condition for the most important vital processes.

This conclusion is arrived at by a consideration of the fact that even small deviations of the temperature of the body beyond the stated limits (36° C. to 38° C.) are accompanied by important dangers. The numerous processes which go on in the body, and which are akin to fermentation, explain these dangers; at a temperature of 42·6° C. coagulation within the blood vessels com-

¹ Heidenhain, *Pflüger's Archiv*. Vol. iv. p. 558. Körner, 'Beiträge zur Temperaturtopographie des Säugethierkörpers.' Inaugural Dissertation. Breslau, 1871.

mences (Weikart), and at 49° C. heat-rigor commences in the muscles (Chapter VIII.)

Low vegetable organisms can bear temperatures as high as 60° (Hoppe-Seyler). Low temperatures, even as low as the freezing point of water, may be borne continuously by cold-blooded animals, yet their tissue-changes stop and their activities also well nigh cease. Warm-blooded animals die of cold as soon as their temperature has sunk to a certain extent (about 19° C.) (Before death, however, the frequency of the pulse and the movements of the intestines diminish, as in hibernating animals, enormously, and the central nervous organs become incapable of performing many acts, *e.g.* the convulsions of asphyxia cannot occur (Horwarth).)

If the process of cooling does not reach this limit, the animal may, if suitably warmed, be awakened out of the soporific condition (which corresponds to hibernation). If the temperature of the body be not lowered more than 20°–18° C., animals possess the power of getting warm again spontaneously as soon as they are removed from the influence of cold and placed in a medium temperature. Even below these limits, the heat of the body may be spontaneously restored if artificial respiration be kept up (Walther; Horwarth has brought back to life animals whose bodies had been cooled to 5° C., by simply exposing them to heat.)

Accordingly the organism possesses numerous contrivances for maintaining its temperature within certain limits.

The most important of these are the following:—

1. Such arrangements as regulate the *elimination* of heat:

a. The sensation of a diminished or increased temperature (sensation of cold or heat, Chap. X.) leads man in the first case to surround himself with bad conductors of heat (thick clothes, wool, silk), and in the second with good conductors (thin clothes, linen), or even to use extraneous means (cold baths), to get rid of some of the body heat. *b.* Increased temperature increases the activity of the heart (p. 118) and of respiration (p. 200); the former leads to an increased fulness of the capillaries, amongst others of those of the skin, and consequently to a rise in the temperature of the latter organ, and to an increased loss of heat by conduction and radiation. Thus, when the heat of the body increases, the skin becomes turgid, warm, and moist; when the temperature falls, on the other hand, the skin shrinks, and becomes cold and dry. Increased respiratory activity augments the loss of water from the respiratory passages.¹ The secretion of sweat is, moreover, either occasioned or increased in quantity by an increased fulness of the vessels of the skin, and the rapidly evaporated sweat consumes an extraordinary amount of heat. In summer, when the surrounding air is of nearly the same temperature as the body, this is almost the only way in which the heat of the body is lost. *c.* Cold causes contraction, and heat causes dilatation of the small arteries (p. 112), especially of the skin. This must exert the same regulating action as the phenomena referred to under *b.*

2. Such arrangements as exert their action in regulating the

¹ The possible generation of heat in the lungs cannot be materially increased by increased respiration without a corresponding increase in the quantity of oxygen used.

production of heat: *a.* An involuntary and direct increase in the amount of heat produced on exposure to cold, which takes place in a manner yet unknown, has been suspected to occur by some (Hoppe, Liebermeister,¹ Röhrig and Zuntz²), especially because under the influence of the cold bath the temperature of the axilla at first rises, whilst the excretion of carbonic acid is increased; others, however (Senator,³ Winternitz, Riegel⁴), suppose the first phenomenon to be due to an arrested loss of heat owing to the contraction of the blood vessels of the skin, whilst the increase of tissue-change, evidenced by the increase in the excretion of carbonic acid, is not a constant phenomenon, and may be replaced by a decrease; in any case it need not be associated with an increased production of heat. *b.* A diminution of temperature (cold) increases the feeling of hunger, and increased consumption of food augments the production of heat. *c.* When the body is exposed to cold the need for muscular exertion is felt,—such as walking backwards and forwards, work—and this raises the temperature in a twofold manner; further, there occur certain (presumably reflex) involuntary muscular movements (shivering, chattering of the teeth), both of which actions can be executed voluntarily with the object of generating heat.

Small individuals, whose losses of heat are constantly greater than those of larger individuals, eat more and move more actively.

The efficiency of the regulating arrangements in providing against loss of heat, especially in the case of man, is but small, so that clothing, fuel, and movements of the body are the most efficacious protection which he possesses against the cold.

Fluctuations in the Mean Temperature.

It yet remains to be stated that fluctuations of the mean body temperature (blood-heat) occur within the normal limits, *i.e.*, within such limits as not to call into action the regulating apparatus of the body; and further, to point out what relation these fluctuations bear to the functions of the body and the mode of living. As the heat-producing processes, as a whole, yield carbonic acid nearly in proportion to the heat generated, the fluctuations of heat coincide very nearly with the fluctuations in the carbonic acid excreted.

The following circumstances cause a high temperature:—muscular movements; abundant glandular secretion, especially of bile (hence the calorific value of digestion); great energy of the whole material exchanges of the body, as in persons of the male sex, of strong constitution, of adult age, &c.; morbidly increased material exchanges, such as probably exist in fever (the excretion of urea

¹ Liebermeister, 'Untersuchungen über die quantitative Veränderungen der Wärme-production.' *Archiv. f. Anat. u. Phys.* 1860, 61, 62.

² Röhrig u. Zuntz, 'Zur Theorie der Wärmeregulation und der Balneotherapie,' *Pflüger's Archiv.* 1871.

³ Senator, *Virchow's Archiv.* Vol. xlv. p. 351; vol. l. p. 354.

⁴ Riegel, *Deutsches Archiv. f. Klin. Med.* 1872, vol. ix. Heft 6.

is here increased, and before the rise in temperature occurs, so that the former phenomenon cannot be explained by the latter, Naunyn¹). Circumstances of an opposite nature to the above often cause low temperatures, as do also diseased conditions, which restrain the consumption of oxygen (such as some diseases of the lungs, starvation, &c.)

Further, a diurnal fluctuation of the temperature of the body occurs, independently of the digestive process, which appears to be due to variations in the energy of the oxidation-processes connected with particular periods of the day.

Not only can the mean temperature of the body be affected in a lasting manner by the processes which generate heat, but likewise by those concerned in its dissipation from the body: thus, *e.g.*, the body-temperature is very much influenced by the state of contraction of the blood vessels of the skin, and therefore by the state of excitation of the vaso-motor centre; as the latter is increased in fever, the high temperatures of fever may in part be thus explained (Traube).

The heat of the blood diminishes when sensory nerves are irritated (Mantegazza, Heidenhain²), apparently through the agency of the medulla oblongata; for when the medulla is excited directly the same results follow. This effect is due to an acceleration of the blood current and a consequently increased loss of heat (Heidenhain).

From the facts which have been stated it is easy to explain the increase of temperature which follows irritation of the spinal cord (Tscheschichin³), and the decrease caused by division of the spinal cord, as well as by paralysis of the vaso-motor nerves brought about by poisons (nicotine, curare). We conclude that an increased elimination of heat does take place in the latter circumstances from the fact that when the animals subjected to experiment are placed in a warm medium, section of the spinal cord (according to some authors) leads to a rise in temperature.

Hybernating animals possess during the period of hybernation a very low temperature. In them the production of heat, as well as the loss of heat, is reduced to a minimum, by an extraordinary slowing of the circulation.

APPENDIX.

Immediately after death a temporary rise of temperature is frequently observed (post-mortem rise in temperature). According to some this rise is due to the formation of heat which attends rigor mortis, whilst others account for it by supposing that when the circulation ceases, whilst the loss of heat is very materially delayed, the production of heat in the different organs continues for some time after death (Heidenhain).

¹ Naunyn, *Archiv. f. Anat. u. Physiol.* 1870, p. 164.

² Heidenhain, *Pflüger's Archiv.* 1870.

³ Tscheschichin, *Deutsches Archiv. f. Klin. Med.* 1867, vol. ii. p. 598.

CHAPTER VIII.

THE ENERGY OF MECHANICAL WORK (MOVEMENTS OF THE BODY).

THE liberation of energy in the form of motion is far less frequent in the animal body than the formation of heat, and is connected with certain definite apparatus. This apparatus, wherever found, consists of simple or metamorphosed cells, or constituents of cells. The phenomena of motion have been proved to occur in the following situations in the human body: 1. In muscular fibres, striated and smooth. 2. In lymph-corpuscles and the corpuscles resembling them (colourless blood-corpuscles, connective-tissue corpuscles, mucus-corpuscles, pus-corpuscles, &c.) 3. In ciliated cells. 4. In spermatozoa. 5. In cells exhibiting molecular movements. To these must be added the contractile masses of many simple organisms. Finally, the processes of formation, growth, division, &c., may be regarded as movements. The movements first mentioned differ, however, from those just given by their much greater rapidity, which renders their direct observation possible; whereas the processes of growth take place so slowly as to be only recognisable by their effects after considerable intervals. The former, also, cause only transitory changes of place and form, after which the parts set in motion return approximately to their previous condition; while the latter lead to permanent alterations. The latter are referred to in the Fourth Section of the work.

The above-mentioned organs, some of which are entirely, and others in part, contractile, have, as far as they have been investigated, certain characteristics in common, apart from contractility itself, which point to an essential substance, common to all. This substance appears throughout the animal kingdom, and in many vegetable organisms. It was formerly termed 'sarcode;' but now in general it is called 'protoplasm.' It may, therefore, be stated as a general law, that active movements only occur where protoplasm is found. The properties of protoplasm will be most fittingly described in connection with the physiology of the most important and most thoroughly investigated of the motor apparatuses of the body, viz. the muscles, which will now be considered.

I. THE MUSCLES.

Muscles are essentially distinguished from almost all other motor-structures by the fact that in them motion only occurs after the operation of a discharging force, the existence of which may be demonstrated. This discharge originates, as a rule, in the nervous system.

The existence of automatic muscular movements has been recently maintained (Engelmann: see Smooth Muscle).

Two kinds of muscles are distinguished, chiefly from the arrangement of their histological elements, viz. the striated and the smooth. The physiological properties of both are, as the following consideration will show, essentially the same, although many distinctions appear in the details.

A. *Striated Muscles.*

Transversely striated muscles are placed wherever energetic movements occur. With few exceptions all such movements, and consequently the activity of all transversely striated muscles, are dependent upon the will. Striated muscles are therefore also called voluntary muscles. The heart, whose striated fibres differ in other respects also from those of ordinary voluntary muscle, forms the chief of the exceptions.

Striated muscles form for the most part long roundish cords, or sometimes flat expansions, of a reddish-brown colour, which exhibit a coarse longitudinal fibrillation. They are attached to the parts to be moved (bone, cartilage, &c.) either directly or by means of bundles of connective-tissue (tendons). They are surrounded by strong sheaths of connective-tissue (fasciæ); and internally they are divided up into numerous longitudinal bundles by septa of a finer connective tissue (perimysia). A piece of muscle may without difficulty be teased and separated in a longitudinal direction into smaller and smaller bundles of fibres, until what is called the '*primitive bundle*' is reached, after which separation by tearing is impossible. This '*primitive bundle*' is really no bundle at all, but a tube filled with an apparently fluid mass—the proper muscular substance. The wall of this tube (the *muscle-fibre* or *muscle-tube*) consists of a very elastic, completely closed membrane—the *sarcolemma*. The contents exhibit under the microscope fine, regular, *transverse striæ*, caused by rows of little bodies possessing more strongly refractile properties than the ground-substance. These little bodies are doubly refractive (Brücke). The distance between the transverse striæ, while the muscle is at rest, is very

The body thus separated in the process of coagulation is an albuminous body, *myosin*. It is soluble in concentrated NaCl-solution, and is precipitable from such solutions by the addition of more water or more salt. Dilute acids also easily dissolve myosin, and, in doing so, convert it into syntonin.

Spontaneous separation of myosin takes place most rapidly, indeed instantaneously, at a temperature of 40° C. for cold-blooded animals, and of 48°–50° C. for warm-blooded animals. It may also be induced at once by means of distilled water and acids.

The muscle-serum contains the remainder of the constituents, viz.: 1. A number of albuminous bodies which coagulate at various temperatures from 45° to 70° C., that coagulating at about 60° or 70° being ordinary albumin. 2. Various carbo-hydrates: viz. (a) glycogen (Nasse), which is present in especially large quantities in embryos and young animals (Mac-Donnell); (b) the products of the decomposition of glycogen—dextrin (Limpricht), and grape-sugar (Meissner), which are said by Nasse only to appear *post mortem*; (c) inosit, in large amount. 3. Lecithin in all probability, on account of the presence in muscles of the terminations of nerves; this has not, however, been directly proved. 4. Fats in small amount. 5. Free acids, especially sarcolactic acid, in addition to certain volatile fatty acids—formic, acetic. 6. Various amides: viz., creatine (and, according to some, creatinine also, though others incline to the belief that the latter is derived directly from the former), carnine, hypoxanthine (sarcine), xanthine, inosinic acid, and sometimes uric acid, though this is doubtful. 7. A red colouring matter,—in most muscles hæmoglobin (Kühne). 8. Salts, especially salts of potassium. 9. Water. 10. Gases, chiefly carbonic acid.

The above-named constituents are found in the contents of muscle-tubes which have already undergone coagulation. As the latter process, as well as contraction (see below), is connected with certain chemical changes in the muscle which are as yet imperfectly understood; and as the investigation of uncoagulated muscle or muscle-plasma cannot be carried on without the occurrence of this process, the substances just mentioned are not to be regarded as the constituents of unaltered living muscle. All that has been discovered or surmised with respect to them will be stated in the proper place.

In muscle as a whole there are found, in addition, the constituents of the other bodies which help to make up the structure (connective-tissue, vessels, blood, nerves, &c.) Gelatigenous substance, elastin, &c., must, therefore, be added to the above list. The sarcolemma appears to consist of an elastic substance.

The quantitative composition of coagulated beef-muscle is as follows (Lehmann): in 100 parts—water, 70–80; solids, 26–20; insoluble albuminous bodies (among them myosin, the sarcolemma, &c.), 15·4–17·7; soluble albuminous bodies, and alkaline albuminate of potassium, 2·2–3·0; gelatin, 0·6–1·9;

creatine, 0·07-0·14; fat, 1·5-2·3; lactic acid, 1·5-2·3; phosphoric acid, 0·66-0·7; potassium, 0·5-0·54; the remainder of the ash, 0·17-0·26. Carmine has hitherto only been found in the extract of beef (1 p.c. in Liebig's extract, Weidel).

Conditions of Muscle.

The usual condition of living muscle is one of rest; the processes taking place in muscle in such a state are imperceptible except by the aid of delicate instruments. Out of this state of rest muscle may pass, under certain conditions, into other states: 1. Into the state of Contraction. 2. Into the state of Rigor.

Muscular Contraction.

Mechanical Properties of Muscle in a State of Rest.

For the sake of simplicity we shall regard all muscles here as spindle-shaped, and extended in the direction of their length—a form which the majority of muscles have in fact. A muscle is a structure of slight but very perfect elasticity, *i.e.* it is very extensile, slight weights producing a considerable elongation; but it has the power of returning, immediately on the removal of the extending force, to its original length. During elongation there is, of course, a diminution in thickness, but the volume remains about the same (it is said to be slightly diminished—Schmulewitsch). Unlike inorganic bodies, and resembling in this respect all other organic structures, muscle does not elongate proportionately to the extending force; but equal increments of extending force produce a less amount of elongation the greater the degree of tension of the muscle at the time (Ed. Weber). The curve of extension got by taking the weights as abscissæ and the degree to which they extend the muscle as ordinates is, therefore, not a straight line as in the case of inorganic bodies, but approaches an hyperbola (Wertheim). In the living body the muscles are constantly stretched a little beyond their natural length, as is shown by their retraction from their point of attachment when the fibres are cut across. The value of this lies in the fact that, on contraction, the points of attachment and insertion are approximated immediately without any loss of time or energy in gathering up, or rendering taut, the relaxed muscle. In muscles separated from their attachments the muscle-tubes are not usually found extended in straight lines, but in curves and zigzags.

Liberation of Muscular Contraction.

The influences which lead to the contraction of muscles are called *stimuli*; the action which they exert, *stimulation* or *excitation*; and the capability of being acted upon by stimuli, which characterises muscle, its *irritability* [the special form of irrita-

bility possessed by muscle being distinguished as *contractility*]. Inasmuch as the stimuli induce the conversion of potential into kinetic energy, they have the relationship to the latter of liberating forces, and we may, therefore, speak of the liberation of muscular activity by means of stimuli. The normal stimulus for muscle proceeds from the motor nerves which are scattered throughout its substance; its nature is little understood, and will be discussed in the next chapter. There are, however, numerous other muscular stimuli, some of which are the result of morbid conditions, while others may be employed artificially.

For a long time it was thought that muscles were incapable of direct stimulation, i.e. that all stimuli applied directly and with effect to muscle only act upon the muscles through the nerve-terminations contained in them. The following circumstances have, however, decided the matter in favour of the independent irritability of muscle. 1. Portions of muscle containing no nerve-endings, e.g. the extremity of the sartorius of the frog, are capable of excitation by the direct application of stimuli (Kühne). 2. Certain chemical stimuli are incapable of exciting nerves (Kühne); while, on the contrary, certain electrical stimuli which act upon nerves have no effect upon muscle itself (Brücke: Chapter IX.) 3. Substances which have the property of rendering nerves, and especially intramuscular nerve-endings, inactive, do not deprive muscle of its capability of direct stimulation (e.g. the Indian arrow-poison—curare, Kölliker). Moreover, other influences (e.g. excessive cold, interruption of blood-current) induce a transitory state in which intramuscular nerve-terminations are paralysed, while the possibility of direct excitation remains to the muscles. 4. In certain conditions (exhaustion of muscle) local irritation induces contraction only in the immediate neighbourhood of the point of application of the stimulus, without respect to the distribution of the nerves near the spot (Schiff, Kühne). 5. The lower contractile organisms, which agree in the nature of their essential substance with muscle, are quite destitute of nerves. 6. It is, moreover, said that automatic movements occur in the muscles of the more highly organised animals. (Consult the section on Smooth Muscles).

The muscular stimuli with which we are already acquainted are: 1. *The normal nervous stimulus*, which proceeds to the muscle either from the central nervous organ in the production of voluntary, automatic, or reflex movements, or from some point in the course of the nerve supplying the muscle, at which irritation has been applied. 2. *Electrical stimuli*, which will be more fittingly discussed in the chapter on Nerves (Chapter IX.), as their laws of action upon muscle and nerve are similar. 3. *Chemical stimuli*, among which must be regarded in general all those substances which rapidly induce changes in the chemical constitution of the contents of the muscle-tubes. At the point of application they cause rigor as well as contraction. The majority of them act even when in a very diluted condition; especially is this the case (Kühne) with mineral acids (HCl in solutions of 0.1 per cent.), solutions of metallic salts, lactic acid, diluted glycerin, and ammonia even when present in traces in the atmosphere. To the list of chemical stimuli belongs also distilled water, especially when injected into the vessels of muscles. The greater number of these substances have no stimulating action upon the nerves (e.g.

ammonia), or only when very concentrated. 4. *Thermal stimuli*, i.e. temperatures above 40° C., strongly heated bodies inducing contractions very readily on coming into contact with muscle. 5. *Mechanical stimuli*, i.e. some sudden and marked change of form occurring at any point, induced, for example, by pressure, torsion, tearing, extension, &c. The method of operation of these stimuli is as yet quite unknown.

The same intensity of stimulus does not always produce in the same muscle the same effects—it may liberate at different times dissimilar quantities of energy; that is to say, the irritability of a muscle is not always constant. It depends, as far as has yet been discovered, upon the following circumstances: 1. It is greatest in any organism under a certain medium temperature, and diminishes as the temperature rises or falls above that mean. 2. It is diminished for a time by previous activity: this diminution is called '*exhaustion*' of the muscle, and it may owe its origin to the following circumstances: (a.) The accumulation in the muscle of certain products which are formed in quantity while the muscle is acting, and which are probably not absorbed with sufficient rapidity. These must be supposed to have some prejudicial influence upon activity—a supposition which has recently been confirmed (J. Ranke). The products are carbonic acid and the acid of the muscle, whether it be a free acid or form part of an acid salt. (b.) The deficiency of the special constituents upon the consumption of which muscular activity depends, and which cannot be remedied quickly enough during the active condition. In all probability both causes are concerned in the production of exhaustion. 3. In muscles which are removed from the body, or which are deprived of oxygen by ligaturing their arteries (Stenson), as well as in those of the dead body, irritability diminishes after a slight period of exaltation, but more quickly in warm than in cold-blooded animals. The diminution in irritability occurs *pari passu* with the development of rigor, is accelerated by the same circumstances, and has entirely disappeared by the time that rigor is complete. 4. All influences which essentially modify the normal composition of muscle-substance in the living body diminish and tend to destroy irritability. 5. If irritability has been much diminished by any of the above means except the last, and rigor has not yet occurred, it may in a certain sense be recovered by passing for a long time a strong and constant galvanic current through the muscle in the direction of its length (Heidenhain), the probable explanation of which will be given in Chapter IX. when speaking of the modifications of nervous irritability. 6. Another means of restoring irritability when it has been diminished by ligaturing the arteries supplying a muscle, is by renewing the circulation, which, however, only operates so long as rigor is incomplete.

As the majority of solutions, and even distilled water, have a stimulating and destructive action upon muscle, there are but few indifferent liquids in which it undergoes no change. Such are dilute solutions of NaCl (0·6 per cent. being the most favourable, O. Nasse), or of other sodium salts, the per-centage strength which is most favourable being determined by the molecular weight of the salt (Nasse). Less favourable than these, but less destructive than distilled water, are solutions of boracic acid (1·5-2 per cent.), and of arsenious acid (Brücke).

The Phenomena of Muscular Contraction.

Muscular contraction consists in a shortening of the muscle in its longitudinal axis, *i.e.* in the axis of its fibres, and of a simultaneous transverse thickening; this change of form takes place with so much energy as to be able to overcome considerable resistances which are opposed to it. Such resistances are nearly always opposed to the shortening, and consist of forces which draw away from one another the two ends of the muscle; the most common case, to which all others may be referred, is that in which a load hangs from the muscle which is supposed to be suspended. By the shortening of the muscle the load is lifted, and the mechanical work performed in the act is expressed by the product of the load into the height to which it is lifted [and which will be shortly designated '*the lift*'].

The fibres which in relaxed muscle are often bent in zig-zags become stretched in the process of contraction (Weber). The transverse *striæ* become approximated. Besides being perceived by direct observation, this approximation reveals itself by the fact that the diffraction-spectrum, which muscle exhibits, like a *Nobert's plate*, when light passes through it, becomes broader during contraction (Ranvier). According to the various views of the structure of muscle, the statements concerning the arrangement of the muscular elements during contraction differ; whilst nearly all observers agree in stating that the anisotropic parts are approximated in the direction of the axis, there is a dispute as to whether they themselves become shorter and thicker.

The diminution in length and increase in thickness of a muscle on contracting are connected with a diminution in volume—a species of condensation. This may be proved by suspending a muscle in a vessel, provided with a narrow, upright tube protruding through the cork, the whole of which is accurately filled with a fluid. When the muscle is stimulated to contraction the fluid sinks in the narrow tube (Erman, Valentin).

Muscle when contracted is also less elastic, and therefore more extensible, than when at rest (Ed. Weber¹).

After each simple stimulation directly applied, a single and rapid alteration in form occurs in the muscle, and is called a *simple muscular contraction*, or more shortly a *contraction* [a *twitch* (Burdon Sanderson)]. The diminution in length does not take place immediately on the application of the stimulus, but is postponed for the space of about $\frac{1}{100}$ th of a second, during which

¹ Weber, art. 'Muskelbewegung,' *Wagner's Handwörterbuch d. Phys.* Vol. jii. p. 54.

time the muscle is, to all appearance, still at rest: this is called the '*period of latent stimulation*' (Helmholtz), or the '*latent period*' of muscular contraction. At the end of that time active contraction commences, at first with increasing, but afterwards with diminishing rapidity, and continues until a maximum is attained. The contracting forces then cease gradually to act upon the muscle, which is thereupon extended by means of the attached weight, at first quickly, but afterwards more slowly, to its previous length. If the muscle is not acted on by any weight, not even its own (as, for example, when it rests upon a surface of mercury), it retains approximately the form it had at the instant of maximum contraction (Kühne); and, if the weight is but slight, it does not completely attain its original length (Hermann). If we imagine the upper extremity of a vertically suspended muscle to be fixed, and an upright plate to travel quickly and regularly in a horizontal

FIG. 1R.

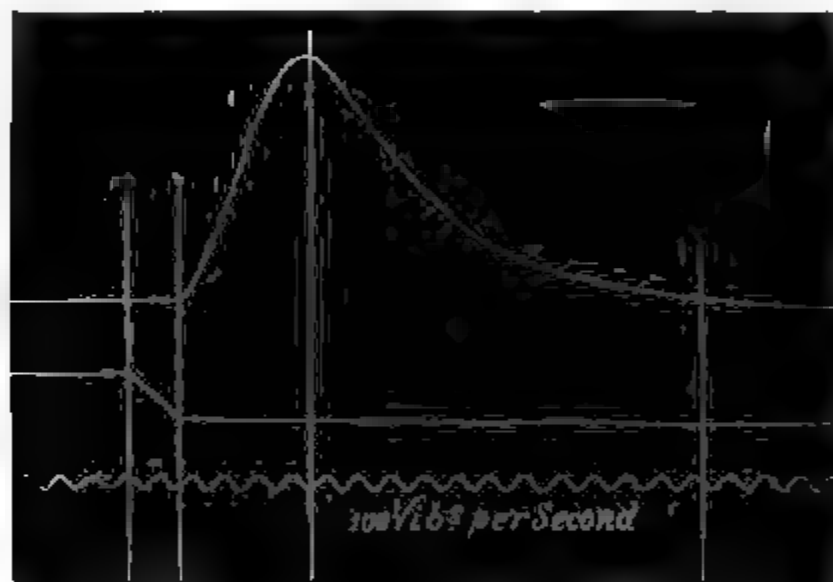


DIAGRAM OF A CURVE OF A 'SIMPLE MUSCULAR CONTRACTION.'
(To be used from left to right.)

direction in front of the lower, a curve would be described upon the plate during the contraction of the muscle, the abscissæ of which would represent the times, and the ordinates the degree of contraction. Such a curve presents the following points of interest: From the instant of stimulation it runs at first for some distance upon the abscissa-line (latent period—period of latent stimulation); it then rises, being at first convex, but afterwards concave towards the abscissa-line, until it reaches a maximum, after which, if the weight have been sufficiently large, it gradually falls again to the abscissa-line (Helmholtz).

[Above is shown diagrammatically the curve of a simple muscular contraction as traced by a lever connected with a muscle on a blackened cylinder revolving with considerable velocity. The upper

line is supposed to be traced by the point of a lever connected with the muscle. The middle line is traced by a lever which marked the moment of stimulation of the muscle. The lowest sinuous line is traced by a tongue of metal attached to a tuning-fork vibrating 100 times per second. The moment of the stimulation is shown by the depression in the middle line, at the point where the first vertical line cuts it; the rise of the upper line is seen to have occurred a short time after stimulation; this interval—the ‘latent period’—is seen, by referring to the tracing of the tuning-fork, to have been about one and a half hundredth of a second.]

The time occupied in the evolution of energy in a muscle after stimulation may be discovered in two ways (Helmholtz):—

1. A muscle to which a slight weight is attached is allowed to contract freely, in which case the distance through which the attached weight is lifted increases and diminishes in the same ratio as the contracting force. The muscle is suspended vertically, and its lower extremity is attached to a lever provided with a pen arranged in such a manner as to mark, when the muscle contracts, upon a surface moving with uniform velocity in a horizontal direction in front of it. This moving surface is either in the form of a cylinder rotating evenly about a vertical axis, as in Helmholtz’s myograph, or of a smooth plate fixed to the extremity of a long pendulum, as in that of Fick. A curve is in this manner produced, of which the abscissæ represent the time, and the ordinates the degree or extent of contraction. As the latent period occupies an appreciable portion of the line traced by these means, the instant of stimulation must be indicated on the recording surface by some mark. This is most easily done by causing the moving surface itself in passing some point in its course to effect the stimulation, say by closing a current. Instead of making use of the shortening of muscle for the production of a curve, the thickening which it undergoes on contraction may, by a suitable apparatus, be registered in the form of a curve, which, as might be expected, agrees with that produced in the above manner (Aeby, Marey). This method is applicable to the muscles of a living man.

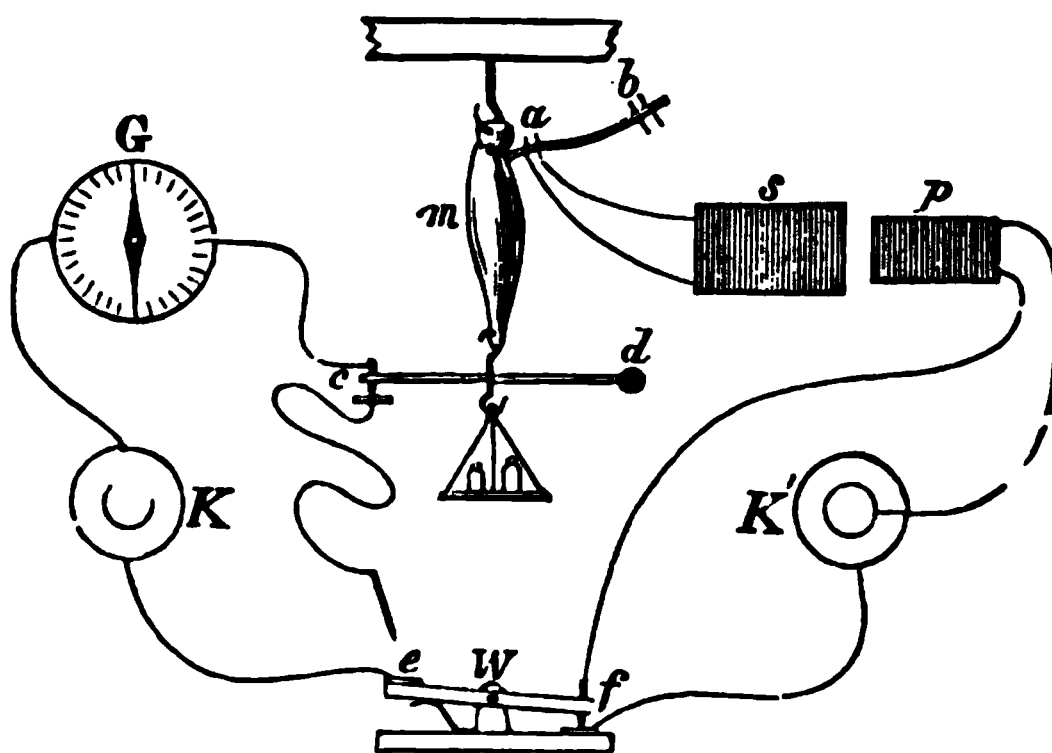
2. Contraction is not allowed to occur, but is hindered by means of weights placed in a scale-pan attached to the lever *dc* (fig. 19), which is supported in such a manner that the weight cannot act upon the muscle while it is at rest, but only when it tends to contract. Each weight placed in the scale-pan (*‘overload’*) keeps the muscle in the position it occupies when at rest, until the contracting force (energy) attains an intensity equal to that of the *overload* (*‘Ueberlastung’*). As the contracting force is evolved gradually after stimulation, the time intervening between stimulation and the lifting of the weight from its support, *i.e.* the striking of contact at *c*, is greater the heavier the weight. If the value of the overload is = 0 the time from the application of the stimulus to the raising of the lever corresponds to the latent period. A degree of overloading is at last attained, which prevents any movement of the lever by the muscle, and therefore represents the limit to the evolution of the contracting force. The measurement of the time from the moment of stimulation to the raising of the weight (*i.e.* to the breaking of contact at *c*) is effected by the method of Pouillet, according to which it is registered by the deflection of the needle of a galvanometer *G*, the current of which is made at the instant of stimulation, and broken at *c* when the weight is raised. The coincidence of closure of the galvanometer-current and the stimulation of the muscle is accomplished by pressing the point of the wire against the plate *e* of the commutator *w*, whereby the current from the battery *K* is closed, while that from the battery *K’* connected with the primary coil *p* is broken at *f*, in consequence of which an opening induction shock is transmitted by the wires from the secondary coil *s* to the muscle.

If the times registered by the above method be taken as abscissæ, and the

corresponding weights as ordinates, a curve presenting energy is obtained, which agrees with the ascending portion of the ordinary muscular curve, got by means of the myograph. The latter, however, deviates slightly from the former, on account of the weight suspended to the muscle in myograph-experiments in order to keep it extended (Klünder). The curve representing energy may also, by proper arrangements, be obtained directly (Fick).

If an unweighted muscle be allowed to contract, and in the midst of contraction brought to a standstill suddenly by means of a weight, it will be found that a smaller weight is required to effect this according to the extent to which contraction of the muscle has already gone. The force of a muscle, therefore, diminishes during contraction, and is equal to nothing at the end of it. In order to show this, the weighted lever is so arranged by placing it nearer to the fixed extremity of the muscle, that a certain extent of contraction must have taken place before the muscle begins to act upon it (Schwann, Hermann).

FIG. 19,



SCHEMA OF EXPERIMENT FOR DETERMINING THE INFLUENCE OF AN
'OVERLOAD' UPON THE TIME OF CONTRACTION OF A MUSCLE.

Certain muscles have the characteristic that their contraction proceeds very slowly, and, in consequence, gives rise to a very extended muscle-curve: such, for example, are the muscles of the tortoise and of the heart (Marey), the latter forming the transition in rapidity of contraction between striped and unstriped muscles (see below). Cold, exhaustion, &c., hinder the progress of contraction (Valentin, Klünder) and diminish its extent (Volkmann).

The return of a muscle to its initial length only occurs completely when sufficient extending forces act upon it (Kühne, Hermann). The persistence of contraction, in spite of extending forces, is noticed when the muscle is highly fatigued, or about to pass into the condition of 'rigor,' or when it is directly and very powerfully stimulated (Tiegel), or when its properties are modified by a muscular poison, such as veratria (V. Bezold).

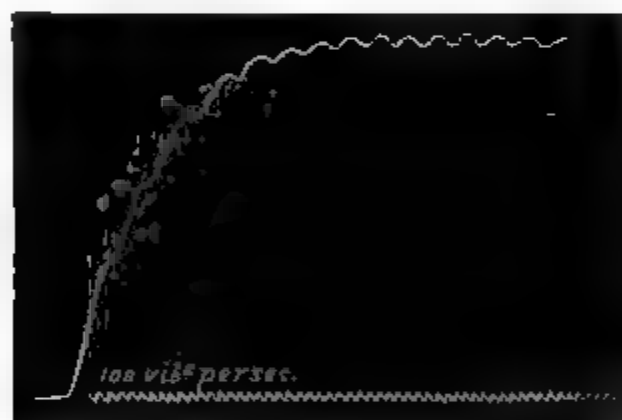
If two stimuli follow one upon the other so quickly that the contraction induced by the first, although it has got past the

latent period, has not reached its maximum before the second commences to operate, their united result is to produce a stronger contraction. That is to say, the second stimulus operates just as if the contracted form which the muscle had when it began to act were the natural form of the muscle (Helmholtz). From this it is evident that the maximum of contraction under the most favourable circumstances may be doubled, viz. when the difference in time between the two stimulations equals the duration of a single contraction from its commencement to its maximum.

Further, if a series of stimulations are brought to bear upon a muscle at very short intervals of time, no opportunity is afforded to the muscle of regaining its normal extension between any two of them; and, in consequence, it retains its contracted form during the whole series: this condition is called 'tetanus.'

[In fig. 20 is shown the curve traced on a blackened travelling surface by a lever attached to a muscle which is thrown into a state of tetanus. The stimu-

FIG. 20.



CURVE OF TETANUS.

lations in this case succeeded each other sufficiently rapidly to prevent the muscle relaxing, and yet not so rapidly as to conceal the influence of each stimulation. Had the stimulations been even more frequent, the 'fusion' of the effects of the successive stimulations would have been complete, and an unbroken curve would have been traced.]

All continued muscular contraction, of which the body presents so many examples, must be regarded as tetanic, i.e. as being produced by a series of stimuli following closely one upon another (Ed. Weber). That such continued contraction is to be looked upon as the result of a series of single contractions appears evident; firstly, because of the phenomenon of 'secondary tetanus,' to be described afterwards (du Bois-Reymond); and, secondly, from the production of the 'muscular murmur.' The latter may be heard by applying the ear or stethoscope to the tetanised muscle of a man (e.g. to a muscle in a state of voluntary contraction); it appears to be a weak murmur in which a distinct note predominates—the muscular murmur or note (Wollaston). The

vibrations of this muscular murmur, when the muscle is tetanised by an induction current, correspond per second with the number of stimuli applied (Helmholtz). As voluntarily tetanised muscles generally emit a distinct sound (of 19·5 vibrations per second), the number of stimuli proceeding from the motor central nervous organs during tetanus by the will must be 19·5 per second (Helmholtz).

If stimuli of a certain strength follow one another very quickly (*e.g.* if more than from 224 to 360 occur per sec.), no tetanus results (Harless, Heidenhain), and only the first produces a contraction (initial contraction, Bernstein). If the strength of the stimuli be increased, tetanus follows.

The best means of tetanising muscle is by using as stimuli a series of frequent electric shocks; such a series, for instance, as is produced by the continual opening and closing of an electric current. In order to study those characters of active muscle for the development of which a single contraction is too fleeting, *e.g.* the chemical changes during activity, the evolution of heat, the negative variation of the muscle current, which the galvanometer, on account of the inertia of the needle, does not show in the case of a single contraction, it is best to tetanise the muscle experimented upon.

The first sound of the heart is, according to some, an instance of a muscular murmur of the usual pitch (Natanson, Haughton); ventricular systole would, according to this view, be a tetanic contraction. The muscular murmur may be heard, preferably at night, by stopping the ears with wax, and contracting the muscles of mastication. The depth of the muscular note was formerly given at from 36-40 vibrations per second (Natanson, Haughton, Helmholtz). When it became possible to determine it more exactly by the method given below, it was fixed at 19 vibrations per second—the audible tone is therefore the first harmonic of the primary note in the muscular sound (Helmholtz). The dependence of the note upon the number of stimuli applied per second becomes evident to any one who tetanises his own masseter muscle by means of an induction apparatus, the coils of which are placed in a distant room, the note being the same as that emitted by the interrupter of the machine used (Helmholtz). The fact that a muscle when tetanised by stimuli proceeding from the central nervous organs has a tone with an independent and characteristic number of vibrations, was first noticed in the case of an animal, the muscles of which were thrown into tetanus by stimulating the spinal cord, and which then emitted the deep murmur of contracting muscle (du Bois-Reymond). In such a case the note is independent of that caused by the vibrations of the interrupter of the apparatus used. The muscular murmur may also be heard by fixing a frog-muscle, properly weighted, to one end of a short staff, the other end of which is inserted into the ear, and tetanising it by means of electricity. The vibrations may be rendered visible by imparting them, by resonance, to a strip of flexible metal or paper (Helmholtz).

If a limited portion of a muscle or of a muscular fibre be thrown into the active condition by the application of a stimulus, that condition travels, in the form of a rapidly progressing wave, over the whole length of the muscular fibres implicated. The rapidity of this propagation is in the case of the frog's muscles, about 3 metres per second (Bernstein, Hermann); in the case of the rabbit's muscles, from 4 to 5 metres per second (Bernstein and Steiner). It diminishes under the influence of cold, and

especially when the muscle is fatigued or dying. In the latter case the transmission of contraction may not occur, so that the shortening and thickening remain as a swelling, limited to the stimulated spot ('idio-muscular contraction').

The rate of propagation of contraction is measured (Aeby) by causing two portions of muscle, situated at different distances from the point at which the stimulus is applied, to register their changes in thickness, and then ascertaining the latent period for each. If, on the other hand, the latent period is determined for the same part of the muscle, when the point of stimulation is near and distant from it, the rate of transmission of stimulation is ascertained, this being probably identical with the rate of transmission of contraction (Hermann). An idio-muscular swelling forms upon the stimulated spot on strong direct stimulation of fresh muscle, even though the whole length of the fibres contract together, *e.g.* when a blow is inflicted across the muscles of the upper arm.

On the Amount of Work done by the Contracting Muscle.

1. WHEN THE TRANSFORMATION OF ENERGY WITHIN THE MUSCLE IS AT ITS MAXIMUM.

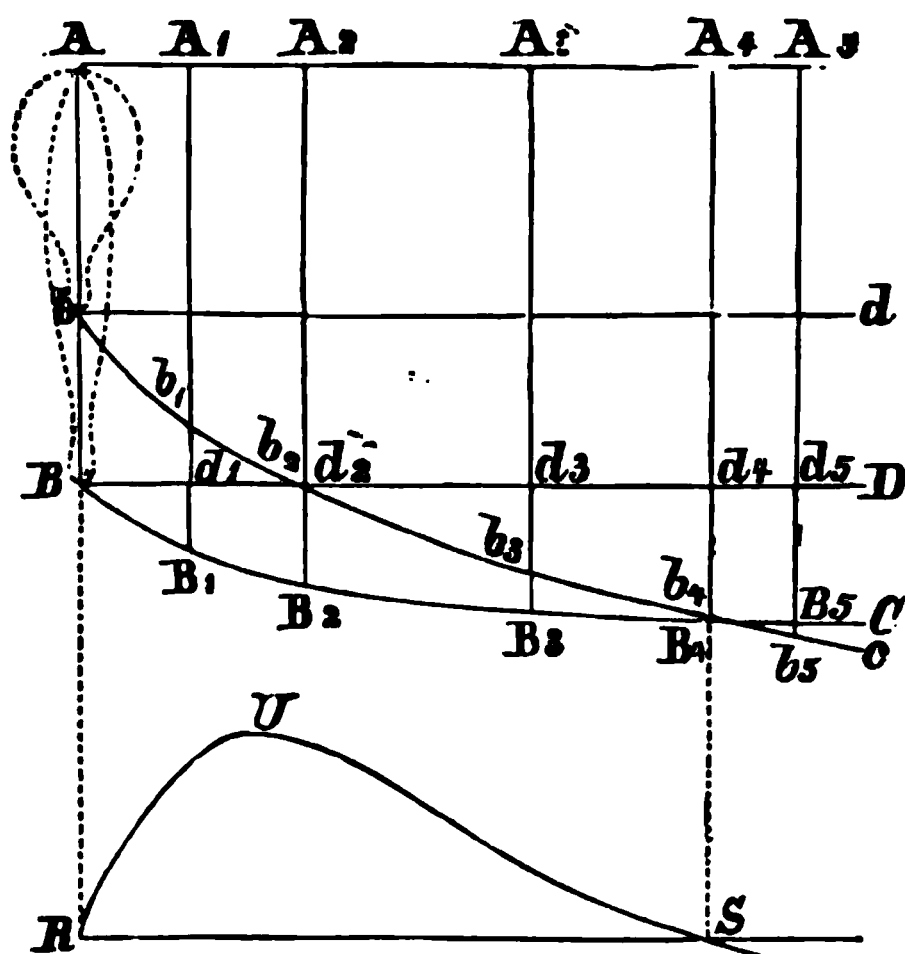
In the first place the most simple case will be considered, that, namely, in which, by as powerful an irritation as possible, as much energy becomes kinetic within the muscle as it is capable of yielding.

An idea may be formed of the mechanical changes which occur in a muscle when it contracts (Ed. Weber) if we imagine that, under the influence of an excitant, and in consequence of the chemical processes which result from its action, the muscle *AB* (fig. 21) suddenly assumes a new natural form *ab*, which differs from the first in being *shorter, thicker, and less elastic*, and which tends to return to its original shape. When the muscle passes from the first into the second, or contracted, form, it behaves exactly as if it had been stretched beyond its natural length, and in virtue of its *elasticity* had tended to assume the new form. The same happens if the muscle when at rest be extended by a weight, only that in this case the length attained is greater than if the same muscle were stretched while contracted. The difference between these two lengths is, of course, the height through which the weight is lifted (*Hubhöhe*), which, for the sake of brevity, we may term the *lift*. The product of the weight raised into the height through which it is raised, *i.e.* the product of *load* into *lift*, expresses the work done by the muscle.

A moment's consideration, assisted by a glance at fig. 21, serves to show that when the extensibility of the contracted muscle becomes considerably greater than that of the muscle at rest, the lift of the muscle will diminish as the load increases,

being with a certain load nothing, and finally becoming negative. That is to say, when the load attains a certain amount, it will no longer be raised on the application of a stimulus to the muscle; and also, as it increases still more, stimulation will cause *elongation* of the muscle, instead of *contraction*. Let AB , in fig. 21, be the natural length of the uncontracted muscle; moreover, suppose loads of various sizes to form abscissæ on the axis BD , and the extensions corresponding to them to be carried down as ordinates; then BC is the curve of extension of resting muscles, and A_1B_1, A_2B_2, A_3B_3 , &c., are the lengths of the muscle corresponding to the loads Bd_1, Bd_2, Bd_3 , &c. Again, let Ab be the natural length of the *contracted* muscle (for a given stimulus); as, now, its elasticity is to a certain extent less than that of the muscle at rest, the curve of extension,

FIG. 21.



bc , obtained in the above manner, will fall more abruptly than BC , and cut it in a point B_4 . As $A_1b_1, A_2b_2, A_3b_3, A_4b_4$, &c., are the lengths of the *contracted* muscle under the different loads, the lines B_1b_1, B_2b_2 , &c., between BC and bc , are the lifts of the muscle on stimulation. It is seen at once that they become smaller and smaller, being at $B_4=0$, and after that point (B_5b_5) negative. That is to say, elongation takes the place of contraction on the application of a stimulus, A_5B_5 extending to A_5b_5 . The work done by the muscle when carrying the various loads is found by multiplying the abscissæ (Bd_1, Bd_2 , &c.) into the corresponding lifts. It is at once seen that this product $=0$ at two points, viz. at B and at B_4 ; that it is greatest a little before the middle position between those two points is reached; and that, on the other side of B_4 , it is a

negative quantity. The variations in the work done may be represented by the curve *RUS*.

In accordance with this theory the stimulus remaining constant and the load increasing, the lifts decrease, following a law which corresponds to the relations between the lengths of Bb_1 , B_1b_1 , B_2b_2 , &c.; it must be noticed, however, that in simple muscular contraction momentum somewhat exaggerates the lift. According to Fick, no amount of loading promotes elongation during activity as Weber maintained. According to Fick's view, the two curves *bc* and *Bc* do not meet, but are asymptotes.

The relations of muscles of the same kind (from the same animal), but of different size, are very simple. The activity of contraction being at its maximum, the weight which a muscle can lift to a given height will increase as its transverse section becomes larger, and, the weight being constant, it will be lifted higher the longer the muscle. The demonstration of this is easy. Let us imagine n similar muscles to be suspended close together in parallel lines; suppose each of the muscles to have attached to its free extremity a unit-weight, which it is capable of raising to a unit-height; a muscular system is thus arranged which has n times the extent of transverse section of one muscle, and which can raise n units of weight through a unit of height. On the other hand, if the n muscles be connected together end to end, and the system suspended by one extremity while a unit-weight is attached to the other, a muscular arrangement is produced which is n times as long as in the preceding case, and which can raise a unit-weight through n units of height. We may render these laws evident by diagrams similar to the one represented in fig. 21, if we hold in view the fact that the extensibility of a muscle is directly proportional to its length and inversely proportional to its cross section.

The amount of work which is done under the influence of the most powerful excitant would appear to be the natural measure of the maximum amount of energy which can become kinetic in a muscle, when its irritability is greatest. The amount of work done is, however, very variable. It depends, for example, upon the weight, as was shown above. Moreover, it follows from Weber's theory, that it is greater if the load be continually diminished as it is being raised (Fick); and, as a fact, many muscles in the body act on levers in such a manner that the moment of the load about the point of support diminishes as contraction proceeds. The maximum amount of work which 1 grm. of frog's muscle can perform varies between 3,324 and 5,760 grammeters (Fick).

Commonly the functional activity of a muscle is determined by ascertaining the maximum power of shortening which it displays on the application of the strongest stimulus. The magni-

tude of this so-called 'absolute muscular power,' expressed in units of weight, is dependent upon the area of its cross section, and is therefore expressed in relation to the unit-area of the section. A square centimeter of frog muscle corresponds to between 2,800 and 3,000 grammes (Rosenthal, and a square centimeter of human muscle to between 6,000 and 8,000 grms. (Henke and Knorz, Koster).

In a muscle separated from the body, the so-called 'absolute power' is determined by the method of 'overloading' which has been described at p. 272. (Other methods depend upon the fact that the weight which represents this absolute muscular power is, according to Weber's theory, the same as would be capable of stretching the unloaded and contracted muscle to the length occupied by it when unloaded and at rest (*i.e.* in fig. 21, the weight corresponding to the abscissa Bd_2); and, in addition, the same as would be necessary for loading the muscle in order that, on contraction, it should regain the length it occupied when uncontracted and not loaded. The determination of this force in man is effected amongst others in the following ways (Weber):—When we stand on tiptoe, or, more correctly, when we rest our weight on the heads of the metatarsal bones, the gastrocnemii muscles, through their insertion into the os calcis, exert an action upon a lever of the second kind, the fulcrum of which is situated at the point of junction of the metatarsal bones to the ground; the weight (of the body) acts upon the point of the foot, through which the line of direction of the centre of gravity passes. If the body be now laden with weights until it is impossible to raise the heel from the ground, then the absolute power of the gastrocnemii is equal to the moment of the weight (body + weights) into its arm, divided by the length of the arm acted upon by the muscles; this value, when found, has only to be reduced in terms of the cross section. The mean cross section of a muscle is determined by dividing its volume (which is equal to its absolute weight divided by its specific weight) by its length.

The method of Schwann measures as it were the absolute power of a muscle in the different conditions of its shortening, when possessing the different lengths between AB and ab (fig. 21): as, however, in the case of the length A_1b_1 , the force found is equal to the weight which can stretch the active muscle Ab to the length A_1b_1 , it is represented by the abscissa Bd_1 . Schwann's experiments afford a means of determining the curve which represents the extensibility of active (*i.e.* contracted) muscle, at least of the portion bb_2 (Hermann).

In the condition of muscular fatigue the absolute power of a muscle diminishes, as well as its power of shortening. When the stimulus is at its maximum, and the load borne by the muscle remains constant, the lift diminishes by an equal amount with every successive muscular contraction, providing that the time which intervenes between successive contractions is always the same. The longer the interval between successive stimulations, the smaller the diminution in the lift. The influence of the time which intervenes between the contractions is most marked when the muscle is in a state of fatigue. The times between the contractions remaining constant, the differences in the contractions become less perceptible as soon as the muscle no longer contracts so as to have the length which it possessed when at rest and unweighted; the curve which represents the magnitude of the muscular contractions, which up to this point is rectilinear, now becomes a hyperbola, which is an asymptote to the curve which indicates the extensibility of the uncontracted muscle.

During tetanus a muscle executes no external mechanical work, as no weight is lifted by it; the weight already lifted to a certain height being merely maintained at that height. As the

chemical changes which go on in a muscle which is in a state of tetanus are greater in amount than in a muscle at rest, we must assume that a tetanised muscle actually does perform work, the muscle losing and immediately thereafter regaining the whole of its tension during the extremely short interval between two successive stimulations; this sudden regain of tension must, whenever it occurs, lead to a development of heat. One must seek for the equivalent of the tissue-changes which go on in the tetanised muscle, in the heat which is generated. The continually recurring changes in the tension of a muscle are probably the cause of the '*bruit musculaire*,' or muscular noise, to which reference was previously made. It has not hitherto been possible, even with the help of the most delicate arrangements, to demonstrate that at the time of the production of the muscular noise the load borne by a muscle is slightly lifted up and down.

2. WHEN THE ACTIVITY OF THE MUSCLE IS NOT AT ITS MAXIMUM.

The lift and the work done by a muscle, when the stimulus applied to it is constant, but of moderate intensity, appear to follow the same laws as hold in the case of the muscle excited by an intense stimulus.

If the strength of the stimulus varies, the degree of muscular activity varies also; the new form which the muscle tends to assume, under the influence of the stimulus, differs, both in elasticity and in length, less from that which the muscle possessed when at rest, the weaker the stimulus. It has not yet been determined according to what law the strength of the stimulus affects the intensity of the active condition of a muscle; the load remaining constant, the lift increases in proportion to the strength of the stimulus, and then remains constant (Fick); the absolute force of the muscle, when the strength of the stimulus is increased, increases at first rapidly, then slowly, and approaches the maximum asymptotically (Hermann).

If the changes in the elasticity of the muscle which correspond with every change in its form were known, one might, as in fig. 21, construct, for every case, the extension curve of the active muscle, and so determine the height to which a weight would be lifted for every weight and for every degree of muscular activity. The relation between changes in elasticity and in form is, however, unknown, and determinations of the height to which a known load is lifted permit of no conclusion being arrived at as to the natural form of the *unloaded* muscle (for the same degree of activity). Although the extension curves of the contracted muscle cannot be constructed *à priori*, yet fig. 21 shows us that the line *bc* approaches more closely to *BC* and is proportionately less inclined to *BC* the smaller the activity of the muscle, and the weaker the stimulus. Hence the differences between the heights to which different weights are lifted must diminish as the strength of the stimulus diminishes, and the weakest stimulus capable of exerting an action must therefore lift to a slight extent as well the smallest as the heaviest weight—in other words, in order to produce the maximum lifting of 1 gramme or 100 grammes, the same

strength of stimulus is required; experiment confirms this conclusion (Hermann).

From what has been stated it follows that a certain stimulus leads to the performance of very varying amounts of work in muscles which are differently weighted: this is explained by the supposition that the effect of weighting a muscle is to convert it into a new body, possessed of more potential energy than before. The influence of the weight borne by the muscle must be even greater than the preceding statement implies, as it exerts an influence on the material exchanges which go on in the muscle. The flow of blood through muscle is accelerated by the dilatation of arteries (Ludwig and Sczelkow, Gaskell), the vaso-dilator nerve fibres, which are mixed with the motor fibres, being excited simultaneously with the latter.

Rigor Mortis.

If a muscle is removed from the blood-current, or excised from the body altogether, it passes—in warm-blooded animals quickly, in cold-blooded animals much more slowly—into a state which is called *death-rigor*. In this condition it is devoid of irritability, it is strongly contracted in the direction of its length, it is less elastic, it has a whitish curdled appearance, and an acid reaction (du Bois-Reymond), and its volume is slightly diminished (Schmulewitsch, Walker). Under the microscope the previously transparent muscle-tubes appear opaque and flocculent, and their contents solid (Kühne).

The appearance of 'spontaneous' rigor is hastened by previous continued activity of the muscle; and by heat, a temperature of 40° C. for cold-blooded animals, or of 48° to 50° C. for warm-blooded animals, inducing it instantly (*heat-rigor*). In the cold the occurrence of rigor is much delayed, not taking place for several days at a temperature of 0° C. It is induced, moreover, by distilled water (*water-rigor*), by acids, even the weaker kinds, such as carbonic acid (*acid-rigor*), by various chemical bodies, and by first freezing and then thawing the muscle.

The action of many of the above-mentioned agents in inducing rigor may take place even when the circulation through the muscle is intact; but a longer-continued and more intense operation is necessary. The effect of the circulation of blood through the muscle is to retard the occurrence of rigor (Hermann).

Cessation of the blood-circulation causes rigor in muscle by depriving it of oxygen; for rigor may be postponed for a considerable time in excised muscles by injecting into their vessels oxygenated blood, a result which does not follow if the blood injected contain no oxygen (Ludwig and A. Schmidt). Moreover, excised muscles through which no blood is passed lose their irri-

tability less quickly in air or oxygen than in gases containing no oxygen (von Humboldt, G. Liebig); but here the difference is extremely small, probably because the oxygen comes into contact only with the external surface of the muscle.

If the muscles after death are in their ordinary position, their shortening during rigor induces a stiffening of the limbs known as 'rigor mortis' or 'cadaveric rigidity,' which only disappears when putrefaction commences, the limbs then again becoming movable. From the rigidity of the corpse the term 'rigor mortis' has been derived.

The position of the limbs in the rigid corpse is chiefly the resultant of the forces exerted by the rigid muscles and by gravity. When rigor commences very suddenly the limbs occasionally occupy the position which they had, owing to muscular contraction, assumed at the moment of death (Brinton, Rossbach, &c.); this condition, however, appears always to be connected with changes in the spinal cord (Falk).

Even in the case of the shortening induced by 'rigor' the lifts corresponding to definite loads and the absolute muscular force can be determined. The former are greater for light loads but smaller for heavy loads than in the case of living muscle under the influence of stimuli of maximum intensity. From the point of view of Weber's theory the natural form of muscle in rigor is therefore shorter, but its extensibility greater than that of active muscle; the absolute muscular force being less in the former than in the latter cases (Walker).

The essential process in rigor is a coagulation of the contents of the muscle-tubes, whereby they become solid (Brücke, Kühne). The coagulated body, the spontaneous separation of which from muscle-plasma takes place at once at a higher temperature, is an albuminous substance, *myosin*. From the observations upon muscle-plasma we must suppose that the contents of the muscle-tubes become first viscid and then gelatinous; and that at last the coagulum, like the coagulum of fibrin in a blood-clot, contracts, thus shortening the muscle, which becomes opaque and yields a juice, the *muscle-serum*. It appears, therefore, that various stages are to be distinguished in the occurrence of rigor, only the last of which are visible to the eye, viz. the opacity and the diminution of length.

Besides the separation of myosin other processes occur, viz.: 1. The already-mentioned acidification, which is the result of the formation of an acid or of an acid salt. The acid may be sarcolactic acid; but glycerin-phosphoric acid is also said to be present (Diaconow). The amount of acid which results from the occurrence of rigor in a muscle is the same whether the latter take place slowly (spontaneous rigor) or quickly (heat rigor) (J. Ranke). 2. An excretion of carbonic acid which depends upon the formation of free carbonic acid. Here again the amount is independent of the method by which rigor is induced. The carbonic acid formed during the occurrence of rigor is, moreover, less the greater the amount the muscle has generated previously by

contracting (Hermann). 3. A diminution in the amount of glycogen present, which is also independent of the manner in which rigor takes place: it has not been discovered what becomes of the glycogen (O. Nasse).

Of the first, imperceptible, stage in the separation of myosin, it may be said that, in all probability, in the case of cold-blooded animals, it takes place very gradually: since a muscle, from the moment of its excision, after a very transitory period of exalted irritability, steadily loses its power of responding to stimulation; it may therefore be said that excised muscle commences at once to pass slowly into a condition of rigor, *i.e.* myosin is separated in a gelatinous form, carbonic acid is generated, glycogen is used up, and an acid appears which gradually changes the reaction of the muscle to test paper. The second stage, however, does not occur until after some time, and consists in the contraction of the coagulum and the shortening of the muscle, thus completing rigor.

A muscle may be reclaimed from the first stage of rigor by allowing blood to flow through its vessels, but not from the second, *i.e.* after the contraction of the coagulum of myosin (Kühne, Hermann). The second stage of rigor may be rapidly induced in the muscle of a warm-blooded animal by ligaturing the arteries conveying blood to it (Stenson), and from this stage it cannot recover by the mere renewal of the interrupted blood-current. More will be said hereafter concerning the nature of this recovery.

By suddenly heating a muscle strongly (as by throwing it into boiling water—scalding) it loses its power of entering into rigor: it neither becomes acid in its reaction under such circumstances (du Bois-Reymond) nor forms carbonic acid (Hermann). Mineral acids have the same effect, and we must therefore distinguish acid-rigor from that which usually occurs (Hermann).

When rigor has become complete the muscle begins to putrefy, in the course of which vibriones are formed, the acid reaction gives place gradually to an alkaline one owing to the formation of ammonia, and ill-odoured gases are given off. Putrefying muscle evolves, even in a vacuum, chiefly carbonic acid, nitrogen, and a little sulphuretted hydrogen. Long before the excised muscle is in rigor in every part, similar, though slighter, putrefactive changes have commenced on its external surface.

Thermic Phenomena of Muscle.

Muscles removed from the body, as well as muscles which retain their connection with it, become hotter during activity (Helmholtz,¹ Béclard), which is, therefore, associated with evolution of heat. The heat is greater the higher the contraction and the greater the load, and is developed not merely during the act of shortening but also during the subsequent relaxation (Heidenhain² with Steiner and Nawalichin). In tetanus the evolution of heat is greater at the time of the initial shortening than after-

¹ Helmholtz, *Archiv. f. Anat. u. Phys.* 1848, p. 144.

² Heidenhain, *Mechanische Leistung, Wärmeentwicklung und Stoffumsatz bei der Muskelthätigkeit.* Leipzig, 1864.

wards; the passage from the elongated to the shortened condition, therefore, causes more heat to be evolved than does the maintenance of this shortened condition (Fick).

That heat is developed in muscle during contraction was formerly only proved in the case of tetanus; lately, however, it has been shown even in the case of individual muscular contractions (Heidenhain).

The determination is made by placing one thermo-electric junction, or one series of such junctions, in contact with the muscle, which is made to contract, whilst another junction or series of junctions is maintained at a constant temperature. (This is most easily effected by placing the second junctions in contact with a second corresponding muscle, which is kept at rest.) In the earlier experiments, needle-shaped thermo-elements were employed, which were either thrust into or passed through the muscle experimented upon, so that the junction was in contact with the muscular substance. In the more recent researches, thermo-piles, composed of a combination of many bismuth and antimony junctions, have been employed, one set of junctions being placed closely in contact with the muscle (Heidenhain).

In frog muscles the heat generated during individual muscular contractions amounts to between $0^{\circ}001$ – $0^{\circ}005$ C.: during tetanus it may be as great as $0^{\circ}15$ C.

It cannot be shown, as was surmised, that the stimulus remaining constant an increase of mechanical work is associated with a diminished production of heat. If the work done be varied by altering the load, the intensity of the chemical process which is initiated by contraction is modified; thus the production of acid, and of substances soluble in alcohol, increases with heavy loads (Heidenhain, Niegetiet and Heppner), and thus one's calculations are not realized: the sum of the heat generated and the work done, which correspond to the chemical changes, varying with the load which the muscle has to lift.

If with a muscle bearing a constant load and subjected to a constant stimulus the work be varied by causing, in one case, the weight which has been lifted by each contraction to fall freely, so that on the whole no useful work is done, and the muscle is heated by the falling of the weight which extends it; and if in another case the muscle be enabled to raise the weight higher and higher by its successive contractions, the weight being supported in the intervals by a ratchet-wheel, so that useful work is done (Fick)—it is found that in the first case the muscle becomes warmer than in the second. It may, however, be remarked that the chemical processes do not terminate at the same instant as the lift, but continue during the process of elongation, during which, as during contraction, they are affected by the tension to which the muscle is subjected. Actually in the first case the muscle produces less acid than in the second (Landau and Pakully); here again the conditions of the experiment modify the chemical transformations, and so also the sum of the work and heat generated.

Naturally, in accordance with the principle of the Conservation of Energy, the sum of the kinetic energies evolved in the muscle must be equivalent to the chemical changes which take place in each case.

Even during the development of 'rigor' heat is generated in muscle, its evolution coinciding in point of time with the act of shortening (v. Walther, Huppert, Schiffer, Fick and Dybkowsky).

The heat developed during rigor is likewise ascertained by thermo-electric methods, one set of junctions being maintained at a constant temperature (Schiffer). Another method consists in placing the bulbs of two similar mercurial thermometers into two muscles, of which the one is yet living, the other in a state of rigor. These muscles are dipped in an indifferent fluid, which is then warmed; when the temperature which produces heat-rigor is attained, the thermometer which was placed in the yet living muscle indicates a sudden rise

in temperature (Fick and Dybkowsky). That heat is developed during *rigor mortis* is proved, in the case of the uninjured dead body, by the fact that after death the body takes a longer time to cool than the body which is artificially heated after cadaveric rigidity has set in (Huppert). The development of heat during *rigor mortis* explains post-mortem rises in temperature; and indeed the occurrence of the latter (in certain cases) first led to the supposition that an evolution of heat is associated with *rigor* (Walther).

Even when a muscle is stretched, a very slight evolution of heat occurs (Schmulewitsch, Westermann).

Electrical Phenomena of Muscle.

If a muscle be cut so as to present a transverse section, and if the two ends of a galvanoscopic circuit, especially one which contains a delicate multiplier or mirror-galvanometer, be applied to the muscle in such a manner that one end is in contact with the transverse section and the other with a point of the longitudinal surface, the galvanometer will indicate the existence of a current (Nobili, Matteuci, du Bois-Reymond). This current passes through the galvanometer in a direction from the longitudinal to the transverse section, and therefore, in the muscle, in a direction from the transverse to the longitudinal section. This, which is called the *muscle-current*, is also obtained if any strip of muscular tissue, however small, obtained by longitudinal division of a muscle, be substituted for the whole muscle in the above experiment, provided that the strip is bounded by a transverse section to which one electrode of the galvanometer is applied, and that the other electrode is applied to the longitudinal surface ('*artificial longitudinal section*'). In this case the artificial longitudinal section bears the same relation to the transverse section as did the natural longitudinal surface ('*natural longitudinal section*') in the former case. It seems evident that an individual muscular fibre would also exhibit a muscle-current.

If a living muscle or a bundle of muscular fibres be taken, and the vitality of the tissue be destroyed over a limited length of the muscle or muscular bundle by caustics, by crushing, or by the application of heat, the muscle or muscular bundle will be divided into living portions, which are separated from one another by a dead portion, which is inserted between the former as an indifferent conductor of electricity might be. In this case every point in the cross line of demarcation between the living and dead muscle, and in general every point in the area of dead muscle, behaves, in reference to the longitudinal surface, as the cross section in the experiments previously alluded to. If such an artificial limitation of the living muscular fibres be also called an *artificial cross section*, we may state that generally, in whatever way it is made, *the artificial cross section of a muscle is negative in respect to the natural or artificial longitudinal section*. The nearer the two poles of the galvanometer are to the centre of the longitudinal

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and cross sections respectively, the greater the intensity of the current which it indicates.

Muscles which are rigid, or which have been killed without 'rigor' being induced, exhibit no current.

Amongst the many necessary precautions which must be taken in conducting these researches, we can only mention here that the animal tissues which are the subject of experiment must not be brought directly into contact with the metallic ends of the galvanometer, or of the wires connected with these; for it is well known that two apparently perfectly similar pieces of metal (*e.g.* two copper wires) when brought into contact with a moist conductor—and all the animal tissues may be considered as such—form a galvanic chain, the current of which must cause a deviation of the needle of the galvanometer.

Pieces of zinc which have been amalgamated do not, however, give rise to a current when they are connected by means of a solution of zinc sulphate; the two pieces of metal behave under these circumstances as if they were 'absolutely similar.' Relying upon this property, the two poles of the galvanometer are connected (in all researches in animal electricity) with two amalgamated pieces of zinc; each of these pieces dips into a vessel containing solution of sulphate of zinc, and from each of these vessels there projects a pad of filtering paper soaked with the same solution. The animal tissue the electro-motive properties of which are to be investigated is now so arranged that it completes the circuit between the two pads, bridging over from one to the other.

The animal structure is protected from the injurious effect which the solution of zinc sulphate would exert upon it by the interposition of an innocuous conductor; this consists of sculptor's clay which, having been dried, is made into a paste of suitable consistence by means of a 1 per cent. solution of common salt.

The employment of these zinc electrodes possesses the additional advantage of preventing the return of the needle after its first deviation, which, if any other method were adopted, would occur in consequence of the *polarization* of the electrodes. Electrodes made of amalgamated zinc plunged into solutions of zinc sulphate are *non-polarizable*.

[In fig. 22 is shown a schema of apparatus which may be used to demonstrate the muscular current. *aa* are two troughs of zinc, the inner surfaces of which have been amalgamated. These troughs rest upon plates of vulcanite (for purposes of insulation); they contain a saturated solution of zinc sulphate. A little pad of filtering paper *bb* is immersed into each trough so as to rest upon the edge, as shown in the schema. Over each pad of paper is placed a little plate of sculptor's clay, as mentioned in the text. Each trough constitutes one non-polarizable electrode, and is connected directly or indirectly with one pole of the galvanometer *A*. If the electrodes be in good order, on connecting their cushions together by some inactive conductor—as, for example, by means of a small strip of the same clay as covers the cushions—no deviation of the galvanometer needle will occur.

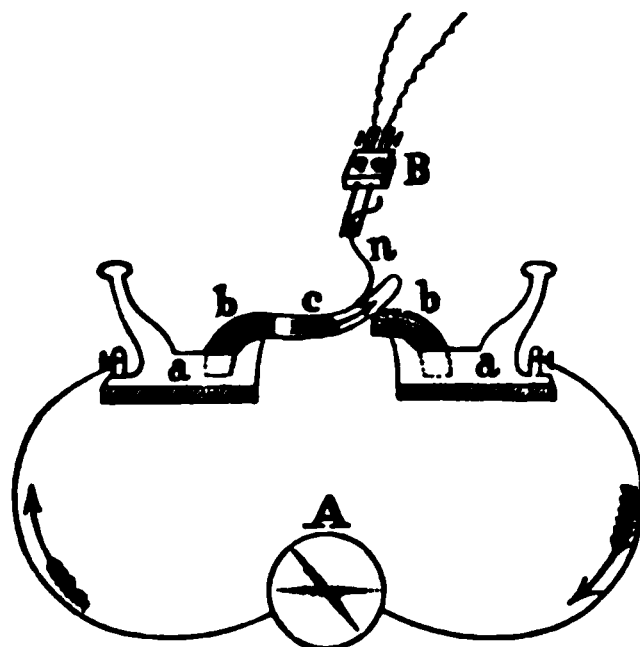
In the diagram a schematic muscle *c* is supposed to have been placed on the cushions, so that an artificial transverse section is in contact with one electrode and a natural longitudinal surface with the other. Under these circumstances a current passes through the galvanometer in the direction indicated by the arrows in the diagram. The nerve *n* is shown to be connected with the muscle *c*, and it is placed over two electrodes *B* connected with the secondary coil of an induction coil. If, after the deflection of the magnet of the galvanometer *A* by the muscular current has been observed, the nerve be stimulated by a succession of induction shocks passing through the two wires *B*, a diminution in the deflection of the magnet corresponding to the so-called 'negative variation' of the muscular current is observed.

Non-polarizable electrodes are often made of other forms than those indicated in the diagram; the galvanometer used in England for these experiments is Sir

W. Thomson's galvanometer. This instrument, when of suitable construction, is capable of easily showing the negative variation corresponding to a simple muscular contraction.]

The muscular current may be demonstrated by methods other than the galvanometric. (1.) By the electro-chemical method, viz. by causing the muscular current to decompose a mixture of iodide of potassium and starch paste; in this case iodine separates at the positive pole and colours the starch blue. (2.) The muscular current may be employed to stimulate nerves, as *e.g.* to stimulate the

FIG. 22.



SCHEMA OF ARRANGEMENTS FOR DEMONSTRATING, BY MEANS OF THE GALVANO-METER, THE MUSCULAR CURRENT AND ITS NEGATIVE VARIATION.

very nerve supplying the muscle ('physiological rheoscope'). In this case it is necessary, as is mentioned in Chapter IX., to allow the current suddenly to break into the nerves. This is effected by suddenly completing a circuit, in the course of which is the nerve of a prepared frog's leg, by interposing the longitudinal and transverse section of a muscle; at the moment of closure of the circuit, a contraction of the leg takes place.

When experimenting with a single muscle the arrangement is as follows:—The nerve belonging to the muscle (which we must imagine to be in contact with the natural longitudinal sections of all the muscular fibres) is suddenly allowed to fall upon the cross section of the muscle; a muscular contraction ensues. (These contractions, without the interposition of metals, were known before the muscular current was discovered.)

Not only are currents observed when the longitudinal and cross sections of a muscle are connected, but also when the electrodes are made to touch two points of one and the same section. A circle embracing a muscle and dividing it into two halves may be called the *equator* of the muscle. Now if in any longitudinal section, natural or artificial, two points be taken for investigation, of which one lies nearer to the equator than the other, it will be found that the former is positive in relation to the latter (which is nearer to the cross section). Similarly, if any two points of a cross section of a muscle be investigated, which are unequally distant from the axis, it will be found that the point which is near the axis is negative in reference to the point which is further away from it (and which therefore is nearer the longitudinal surface).

No currents are observed when the electrodes touch two points which are equidistant from the equator of a longitudinal section, or two points equidistant from the axis of a cross section.

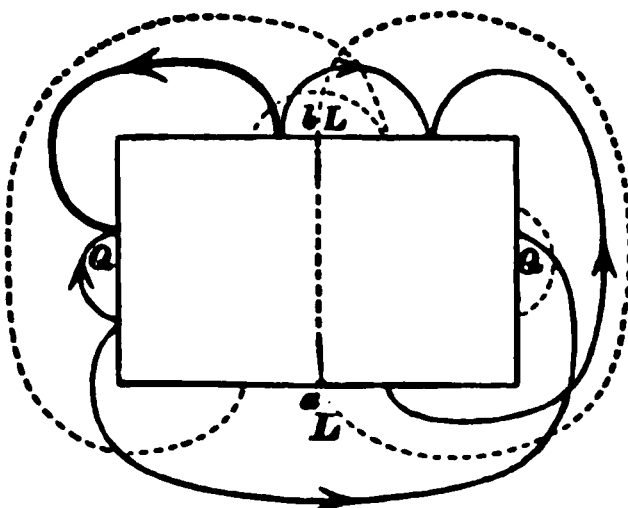
All these laws apply not merely to points on the same cross section, but also to points on different cross sections, and similarly to points on different longitudinal sections. Naturally, the two terminal points of the axis, and any two

points on the equator of a muscle, when connected, do not cause a deflection of the galvanometer.

The currents which are obtained by connecting any two points on a longitudinal section, or any two points on a transverse section, are always very much weaker than those obtained when a point on a longitudinal is connected with a point on a transverse section, and they increase in strength as the difference in the position of the electrodes, in reference to the equator and axis, increases. The currents obtained by connecting two points on the same section are termed *weak currents*, as distinguished from the *strong currents* which pass between a longitudinal and transverse section.

In fig. 23 the rectangular figure represents a piece of muscle: LL are its longitudinal surfaces, qq its cross sections, *ab* its equator. The thin lines show combinations of points (on the same kind of surface) which give rise to weak currents; the thick lines illustrate the production of strong currents; the dotted lines show how different parts of a muscle may be arranged in reference to the electrodes, so as to exhibit no electric current.

FIG. 23.



If an oblique section be made through a muscle, or a vertical section be so altered by pulling as to furnish such a section, a departure is observed from the previously mentioned behaviour, inasmuch as the most negative point of the oblique section does not lie in the middle of it, but is in proximity to its sharp edge; similarly, the most positive points on the longitudinal section do not lie any longer in the equator, but nearer to the blunt edge of the section. In such a *muscular rhomb* a point in proximity to the latter is positive in relation to a point near the former, in spite of the two points being equally distant from the middle. In rhombic pieces of muscle currents must therefore pass from the acute to the obtuse edges which are superadded to the usual muscular current. Such currents are denominated *currents of inclination*.

All the phenomena which have yet been referred to may be explained by the law that each individual muscular fibre exhibits the same (electrical) relations as the entire muscle, viz. that a transverse section through any part of it whatever is negative in relation to the longitudinal surface or section. By this hypothesis the 'strong' currents between the longitudinal and cross sections are explicable. The 'weak' currents are explicable simply by the hypothesis that when a portion of muscle presents cut surfaces, the latter rapidly die down to a certain depth, and are converted by this process of death into indifferent conductors; in this indifferent layer, the muscular current adjusts itself partly, and the electrical tension is so distributed on the surface that the greatest positive tension is in the middle (equator) of the longitudinal section, the greatest negative tension in the middle of the cross section. The phenomena which were described at p. 287 are explained by the fact that a point possessing weak positive tension behaves negatively towards a point of stronger positive tension, and similarly a weakly negative point is positive in relation to a more intensely negative point; lastly, two points which possess the same amount and the same kind of electrical tension do not, when connected, give a current. In an oblique section

the successively projecting active cross sections of the muscular fibres form a kind of battery, whose positive pole is near the obtuse, and whose negative pole is near the acute, edges; the current which is formed in this battery adds itself algebraically to the ordinary muscular current. In this way may be explained the phenomena of the 'currents of inclination.'

The electro-motive force of the current between the longitudinal and transverse sections of a muscle amounts, in the case of a frog, to as much as 0.08 of a Daniell; the electro-motive force of 'currents of inclination' may exceed 0.1 of a Daniell (du Bois-Reymond). All circumstances which produce muscular exhaustion diminish the intensity of the muscular current (Roeber).

In uninjured muscles separated from the body, currents pass from different points on the surfaces, which are of varying intensity and direction. Frequently tendons, *i.e.*, the indifferent conductors which are applied to the natural terminations of the muscular fibres, are negative in relation to the longitudinal section of the former, yet not so powerfully negative as an artificial cross section.

In frogs which have been thrown into a kind of hibernating state by the action of cold, the tendons are frequently electrically neutral, or positive in relation to the longitudinal section of muscle (du Bois-Reymond). *In a perfectly uninjured, unskinned animal, the muscles which are in a state of rest are entirely free from electrical currents* (Hermann¹); the currents originate during the preparation of the muscle in consequence of injurious influences acting upon their surfaces. In frogs, for instance, amongst other such influences, is to be mentioned the action of traces of the caustic secretion of the skin.

The more these injurious influences are avoided, the greater the freedom of the muscle from electrical currents. In muscles which are at rest there are, therefore, no currents except those which are brought about by the negative electric tension of the artificial cross section in reference to the longitudinal section (Hermann).

In order to investigate the electrical currents of the muscles of unskinned frogs it is not sufficient to bring the electrodes, which are connected with the galvanometer, in contact with two points on the surface of the skin, as the skin at any point perpendicular to its surface, from without inwards, possesses electro-motive properties (du Bois-Reymond). These *cutaneous currents*, which are rapidly destroyed by the action of caustic alkalies, must be first eliminated (du Bois-Reymond). If this be done in such a way as to obviate the downward passage of the caustic to the muscle, at any rate up to the time when the experiment is made, the muscles are found to be entirely free from electrical currents (Hermann). Injuries which affect the whole muscular surface always cause the tendons to become negative in relation to the longitudinal surface of the muscle connected with them, for the fibres of the muscle die throughout their whole length, and therefore possess no current of their own, whilst under the tendon are placed the artificial transverse sections of many yet living muscular fibres; this is especially the case when the tendons present merely a thin aponeurotic membrane (as in the case of the gastrocnemius).

The different deportment of the muscles of hibernating animals is most probably to be explained by a certain indifference which they present to slight

¹ Hermann, *Weitere Untersuchungen über den Stoffwechsel im Muskel*. Berlin, Verlag v. A. Hirschwald. 1867.

transient injuries, which entirely agrees with their well-known sluggishness when stimulated.

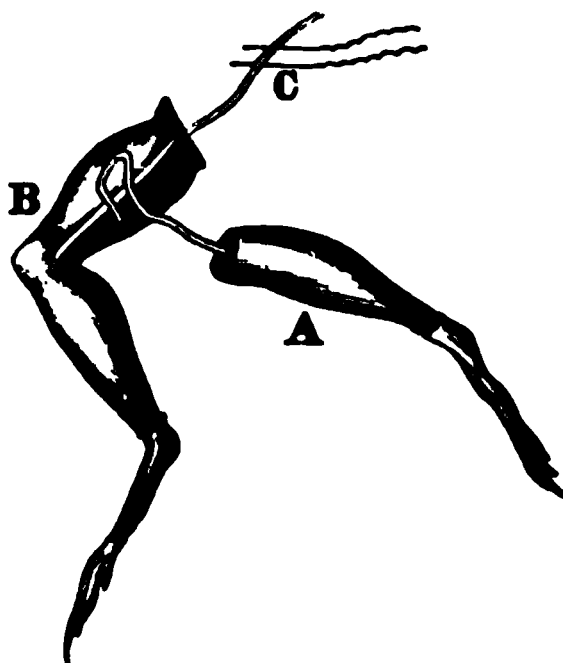
When electrodes are placed in contact with two points on the surface of the limbs of skinned animals, or on two points of the surface of the body generally, currents are observed which are the resultants of the numerous individual muscular currents.

When a piece of muscle which is limited by a longitudinal and cross section is heated to a temperature which does not exceed that required to bring on *heat rigor*, the strength of the muscular current is increased. Cooling the muscle on the other hand diminishes the strength of the current. Warm places in a fibre behave positively in reference to cooler ones. The strength of the current which passes between two points of a muscular fibre is not influenced by the temperature of those portions of the fibre which lie between them. The changes in the electro-motive properties of muscle which are brought about by heat and cold disappear when the original temperature is restored (Hermann).

When the whole of a muscle whose external surface and artificial cross section are connected with the galvanometer is thrown into contraction, there is a diminution of the muscular current, a '*negative variation*' (du Bois-Reymond). The negative variation can be proved, in the case of a single muscular contraction, by causing the change in the intensity of the current to act as a stimulus to the nerves of a second muscle. (The nerve of the second muscle is brought in contact with the longitudinal and transverse sections of the first.) For every contraction of the first there is a contraction of the second muscle ('secondary contraction'). If the first muscle be tetanised, the second one also becomes tetanic (secondary tetanus), a fact which proves that in tetanus there are series of fluctuations in the intensity of the muscular current.

[The subjoined diagram illustrates the mode of proving the 'negative deflection' of the muscular current by means of the 'physiological rheoscope.' B and

FIG. 24.



A are the legs of a recently-killed frog, with a considerable length of each crural nerve attached to the muscles. If the nerve of muscle A be placed on muscle B so that both transverse and natural longitudinal surfaces touch the surface of the muscle, and if then the nerve of A be subjected to a single stimulation, there will follow a simple muscular contraction, not only of the muscle connected

with the nerve directly stimulated—viz. B—but also of the muscle A. On now tetanising B by means of a series of induction shocks applied to its nerve, muscle A will also become tetanic.]

The ‘*negative variation*’ at the most amounts to a cessation of the current, there never being a reversal of its direction (Bernstein, du Bois-Reymond). On the cessation of the state of tetanus the muscular current is weaker than before (‘*innere Nachwirkung*,’ Roever, du Bois-Reymond).

If the electrodes in contact with a muscle are so situated that, during rest, there is only a weak current, or an absence of current, it is observed that the corresponding variation in the intensity of the current, brought about by the contraction of the muscle, is in the first case very small, and that in the second there is no change (du Bois-Reymond).

When the nerves going to a muscle which is uninjured and, either approximately or entirely, free from electric currents, are excited, contraction leads to certain electro-motive manifestations for which no general law has been yet found; the gastrocnemius, for instance, becomes the seat of a descending current which passes between the upper and lower tendons; similarly, during contraction, a descending current is observed in the unskinned lower extremity of the frog. During the voluntary tetanic contractions of the muscles of the human arm there is an ascending current, whilst a similar contraction of the leg is accompanied by a descending current (du Bois-Reymond).

The negative variation of uninjured muscle is distinguished from that depending on an artificial transverse section by the fact of its persistent, unbroken course, and by a more perceptible after-effect; this after-effect, which adds itself to the internal after-effect (*innere Nachwirkung*, see above), must depend upon the fact that tetanus leaves behind it electro-motive effects in the natural terminations of the fibres, which are directed from the longitudinal section towards the tendons (du Bois-Reymond).

If a bundle of fibres be stimulated near one of its terminations, so that a wave of contraction runs along it, it is noticed that the different spots in succession on the longitudinal surface become negative in reference to other spots, there being a negative wave, as it were, which travels along at the same rate as the wave of contraction, viz. about three metres per second (Bernstein¹). At each point the negative state, which first increases and then decreases, lasts about $\frac{1}{300}$ th of a second; it is entirely gone by the end of the ‘latent period,’ which lasts $\frac{1}{100}$ th of a second. Every point in a fibre must therefore first of all undergo electrical changes before contracting (Helmholtz, Holmgren); or, in other words, the wave of muscular contraction is immediately preceded by a negative wave. This wave of negative tension diminishes in intensity as it runs along (Bernstein).

The statement that this negative wave diminishes in intensity

¹ Bernstein, *Untersuchungen über d. Erregungsorgan im Nerven und Muskelsysteme*. Heidelberg, 1871.

as it travels on (Bernstein), appears only to apply to the case of muscle which is dying (du Bois-Reymond).

Formerly the electro-motive changes which occur during tetanus could alone be perceived by means of the galvanometer, because the inertia of the magnet prevented its following the very rapid deflection occasioned by a simple muscular contraction. Lately it has been possible (Hermann), with very light magnets, to obtain powerful deflections even with simple muscular contractions. The duration of the variation is determined by closing for an instant the galvanometer circuit at different periods after the stimulation of the muscle. In order to obtain appreciable results the stimulation of the muscle and the closure of the galvanometer-circuit may be made to follow one another repeatedly in rapid succession and at constant intervals, by causing the necessary electrical contacts to be made at the periphery of a rapidly rotating wheel; such an instrument is the *rotating* or *repeating rheotome*, or '*Differential-Rheotome*' of Bernstein¹. The feeble but successively equal individual effects sum themselves up then so as to produce a permanent deviation. With a very delicate galvanometer repetition may be dispensed with (Fall-Rheotom of Hermann¹).

In the case of an uninjured gastrocnemius, a simple muscular contraction, induced through the nerve, is accompanied by a double deviation ('*doppelsinnige Ablenkung*') which is at first descending and then ascending (S. Mayer).

For the explanation of the electro-motive phenomena of muscle the two following opposed hypotheses have been advanced:—

According to the older of these—that of du Bois-Reymond, which may be designated the 'Pre-existence doctrine' or the 'Molecular theory'—each muscular fibre contains within its interior electro-motive molecules, which are suspended in regular order in a conducting liquid. As these molecules all present positive surfaces towards the longitudinal sections, and negative surfaces towards the transverse sections of a muscle, the former possess positive and the latter negative electrical tension. Every cross

FIG. 25.

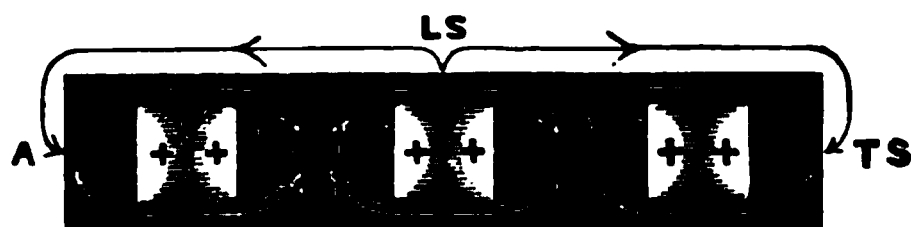


DIAGRAM EXHIBITING THE HYPOTHETICAL ARRANGEMENT OF ELECTROMOTOR MOLECULES IN MUSCLE, AND THE DIRECTION OF THE MUSCULAR CURRENT.

L S is the longitudinal surface, T S is the transverse surface, of the muscle.

section, or the action of caustics, &c., lays bare new negative surfaces. During contraction or, rather, during the latent stage which precedes it, the electric-potential of these molecules changes, so that during the complete contraction of a muscle its current diminishes as a whole, whilst during partial contraction the tract of the muscle which is involved in contraction resembles in its behaviour an indifferent conductor, which now, in virtue of the negative elements of the portion of fibre at rest which are con-

¹ Hermann, 'Untersuchungen über die Entwicklung des Muskelstroms,' *Pflüger's Archiv*. 1877.

tiguous to it, comports itself negatively in reference to the remaining portion of the fibre. In order to explain how it is that the natural terminations of the muscular fibres do not behave (as they ought to do if the above-mentioned scheme held in its entirety) exactly like an artificial cross section, it is assumed that in contact with the ends there is a layer of abnormally arranged ('parelectronomic') elements, which present positive, and not negative, surfaces towards the natural cross section; the greater the number of these elements present the more free is the muscle from electrical currents, or the direction of the current may even be reversed. The development of parelectronomic elements, which, however, are never entirely wanting, is, as must be assumed, promoted by the action of cold, &c.

The other theory (Hermann¹), which may be designated the 'Difference-theory,' because it refers all the phenomena to differences in condition of the same fibre, explains them as proceeding from two actions of contact. There are two sets of circumstances under which muscular tissue comports itself as electrically negative with respect to living, inactive muscle, viz.: (1) when it is dying (entering into rigor), and (2) when it is in activity, or, more exactly, during the latent period preceding contraction. The former case is taken to explain the negative state of every *artificial* cross section of a living, inactive, muscular fibre with respect to its exterior, for, at every artificial cross section between the already dead, and therefore indifferent, portions of the muscular fibre and those which are still living, there is found a layer just in the act of passing into rigor. Hence, all the phenomena of the currents of muscle at rest (p. 285) are explicable. The latter case is cited to explain all the phenomena of muscle after stimulation, especially the diminution of the muscle current on irritation of the injured fibre *in toto*, and the negative condition of the wave of contraction with respect to the rest of the muscle tube.

In order to explain the behaviour of currentless muscles to indirect stimulation (see p. 291), both theories must assume that the ends of the muscular fibres become more feebly excited and less negative than the remainder. The theory of du Bois-Reymond explains this by the definite supposition that the parelectronomic molecules take less part in the effects of irritation than the normal molecules; the theory of Hermann rests satisfied provisionally with the statement of the proposition; the conclusion which has been arrived at from the diminution which the wave of excitation undergoes as it travels on, does not appear to apply to the case of fresh muscle (compare p. 291).

At the time of the terminal after-effect noticed at p. 291, the application of caustic to the tendons causes a more powerful development of currents than before. From this it has been further concluded (du Bois-Reymond) that the waves of excitation, when they reach the ends of the fibres, generate there par-

¹ Hermann, *Weitere Untersuchungen über den Stoffwechsel im Muskel*.

electronic molecules or increase the activity of those already present; further, that the pärelectronic state only depends upon terminal after-effects. And yet it has been impossible to render muscles pärelectronic by tetanizing the body.

The previously-mentioned (p. 289) influence of temperature would, according to du Bois-Reymond's theory, be explained by heat increasing the actual energy of the molecules and cold decreasing it. Hermann's theory assumes a development of electricity by the contact of warmer with colder muscular contents, resulting in the negativity of the latter.

Decisive grounds for opposing the theory of du Bois-Reymond are the following: the complete absence of current in uninjured muscles (p. 289); further, the fact that, after making a cross section, the muscular current is not instantly present in full force, but requires at least $\frac{1}{400}$ th of a second for its development, this time being prolonged under the influence of cold (Hermann¹).

Besides the much greater simplicity of the Difference-theory, it is commended to us by the analogy between the processes of activity and rigor, of which we shall speak more hereafter—an analogy which the theory renders complete. Further, the currents in glands containing blood, as well as those of sections of plants (Buff, Hermann) and of other protoplasmic tissues, may be easily explained by perfectly analogous surmises, whilst they are beyond the reach of the molecular theories.

Concerning the effects of electrical currents upon muscles, reference should be made to the chapter on Nerves (Chapter IX.)

The Chemical Processes of Muscle in a State of Rest.

Very little has yet been discovered respecting the chemical process taking place in resting muscle. As muscular tissue continually effects the conversion into venous blood of the arterial blood flowing to it, chemical processes must occur in it, in which oxygen is used and carbonic acid formed. Certain observations which will be detailed afterwards render it probable that these processes (viz. the use of oxygen and the formation of carbonic acid) are not identical, but only take place side by side.

In excised muscles (and here it is best to use those of cold-blooded animals, as they retain for a long time the properties of normal living muscle) an absorption of oxygen and an excretion of carbonic acid may be detected (du Bois-Reymond, G. Liebig); as also in muscles which have been deprived of blood. These operations cannot therefore be ascribed to the blood in the blood vessels of the muscle, but to the muscular substance itself. As the same gaseous exchanges are exhibited by muscle in a state of rigor as by living muscle (Hermann), they cannot, at least in by far the majority of cases, be considered as the result of functional processes, but must be regarded as due to putrefactive changes which occur especially at the surface of the muscle and at the exposed transverse sections. The amount of such gaseous exchanges in accordance with this theory, being greater the larger the surface of the muscle exposed, and the nearer it is to absolute putrefaction.

As, however, excised muscles retain their vitality under certain circumstances somewhat longer in air or oxygen than in hydrogen or other indifferent gases which contain no oxygen (Humboldt, G. Liebig, Hermann²), it must be admitted

¹ Hermann, *Untersuchungen über die Entwicklung des Muskelstroms*. 1877.

² Hermann, *Untersuchungen über den Stoffwechsel der Muskeln, ausgehend vom Gasechsel derselben*. Berlin, 1867.

that some slight absorption of oxygen connected with the functions of the muscle does take place, which is, nevertheless, too small to account for the gaseous exchanges above mentioned. That the physiological absorption of oxygen in muscles through which blood is passing is much greater than in those which are excised, and so removed from the circulation, may be accounted for by the following circumstances: 1. That, in the former case, a much greater extent of surface is exposed to the operation of the oxygen-carrier, viz. the blood, than in the latter, where the oxygen-carrier is the atmosphere and the surface exposed the external superficies. 2. That the oxygen of the blood, which is combined with hæmoglobin, may possibly have special properties more favourable to its transference to the muscular substance than those of the free atmospheric oxygen. 3. That, in the process of combination of oxygen with the muscle substance, other bodies are needed which are not found in muscle itself, but are conveyed to it by the blood.

Nothing further has been directly made out concerning the chemical processes of resting muscle; but certain conclusions may be drawn from the appearances of muscle during contraction and rigor; reference will, therefore, be presently made to this matter.

The Chemical Processes of Muscle in a State of Activity.

The following chemical processes have been shown to occur in active muscle:—

1. Carbonic acid is formed and given up to the blood, or in the case of excised muscles, to the air. This excretion of carbonic acid is considerably greater during states of activity than of rest. It occurs in excised muscles (Matteucci, Valentin) as well as in those of a living animal or in those through which a stream of blood is artificially maintained; in the latter case the venous blood yields more carbonic acid while the muscle is active than while it is at rest (Ludwig and Sczelkow, Ludwig and Schmidt). The whole body excretes more carbonic acid during periods of activity than when in repose (Regnault and Reiset).

2. Muscles in the body, and muscles through which blood is artificially forced, consume more oxygen during activity than during rest, as is proved by the fact that venous blood contains less oxygen in the former case than in the latter (Ludwig and Sczelkow, Ludwig and Schmidt). The whole organism, also, requires more oxygen during exertion than at other times (Regnault and Reiset); but the difference is much less than that between the amounts of carbonic acid excreted under the same circumstances (Pettenkofer and Voit).

In the case of excised muscles while in action, an increased consumption of oxygen cannot be detected by direct measurement (Hermann).

The absorption of oxygen is not immediately demanded for the purposes of contraction, as muscles are capable of continued exertion in a vacuum or in an atmosphere containing no oxygen. Muscles, moreover, contain no store of oxygen which is capable of removal by exposure to a vacuum (Hermann).

3. During a period of activity muscle becomes *acid* (du Bois-Reymond¹), just as in rigor; probably the acid is the same in both cases.

4. The composition of muscle alters during activity in such a manner that the constituents which are soluble in water decrease in quantity, while those soluble in alcohol increase (Helmholtz²).

The above are the only processes which are certainly known to take place in contracting muscle. Others have, in addition, been mentioned, some of which have been the result of faulty methods of observation, while others have been disproved, or rendered doubtful, by the occurrence of opposite results. The two chief methods of investigation employed are the following: 1. The comparison of the excreta of the organism during rest and exertion; from the list of substances excreted in greater quantity during exertion, conclusions may be drawn as to the substances used. 2. The comparison of the chemical composition of muscles (preferably of the same animal) after periods of repose and of continued exertion. In these experiments muscular exertion may be undergone either (*a*) by muscles in the living animal (as, *e.g.* by inducing the tetanic convulsions of strychnia-poisoning, one limb being kept at rest by the previous division of its nerves), or (*β*) by excised muscles.

There exists, however, in the second method of investigation, a source of error which renders useless the majority of the experiments. It will appear from what is said hereafter that the chemical processes occurring during contraction and rigor are identical in nature; indeed, two similar excised muscles, after having undergone rigor, have exactly the same composition (except as regards the amounts of carbonic acid excreted), whether one has previously been in a state of activity or not. As, now, the requirements of chemical analysis are almost always such as to induce immediate rigor in the muscles under experiment (they have to be at once 'scalded'), we cannot expect to find any difference in composition in the case (*β*) where excised muscles are used; and if differences do appear, no certain meaning can be attached to them. In the case (*a*), on the other hand, where the exertion is undergone by the living animal, the blood current continually removes the products of the material exchanges occurring during the periods of activity, in consequence of which the muscles which have been contracting contain, after rigor, less of those products than those which have been at rest. If, now, we regard as the products of activity those substances only which we can find in increased amount in the muscles which have been active, we shall commit an error (if the occurrence of rigor is not prevented) which will lead us to conclusions exactly the reverse of the truth. The following are the chief theories of the material exchanges occurring in active muscle:—

1. That muscles in contracting *consume* (oxidize) *albuminous bodies*. This theory rests upon (*a*) a supposed increase in the amount of urea excreted during muscular exertion, which, however, does not really occur (Voit); (*b*) a supposed diminution in the albumin contained in muscles during their activity (J. Ranke)—a diminution which, according to others (Nawrocki), is slight enough to be set down to the unavoidable errors of experiment apart from the consideration of the important error above mentioned; (*c*) a supposed accumulation in active muscles of nitrogenous products of oxidation, viz., of creatine (J. Liebig, Sorokin, Sczelkow—the presence of which was not confirmed by the researches of Nawrocki), hypoxanthine, &c. (Scherer); such an accumulation appears to occur under certain circumstances, but not as the immediate result of muscular exertion.

2. That muscles produce, during activity, *grape sugar* (J. Ranke³): the sup-

¹ Du Bois-Reymond, *Ueber angeblich saure Reaction des Muskelfleisches*. Reprinted in his *Gesammelte Abhandlungen*. Vol. ii. p. 8.

² Helmholtz, *Archiv f. Anat. u. Phys.* 1845, p. 72.

³ Ranke, *Tetanus. Eine physiologische Skizze*. Leipzig, 1865.

posed increase is, however, so extremely slight (0·005 per cent.), that, apart from what has been said above, it cannot form the basis for any conclusions.

3. *That muscles produce, during activity, fats* (J. Ranke): this statement is useless as long as the intramuscular nerves, a great part of which is soluble in ether, are not excluded.

4. *That muscles during contraction oxidize volatile fatty acids* (Sczelkow): for the reasons before mentioned the experiments cannot be regarded as affording conclusive proof.

On the whole, therefore, we must reject Ranke's theories, based upon the data given above, that active muscle consumes albumin and forms creatine, sugar (lactic acid), fats and carbonic acid.

With regard to the influence of muscular work upon the total exchanges of the body, the following are the principal statements:—

1 (already mentioned). The interchanges of gases increase during activity, the diminution of CO_2 more, however, than the absorption of oxygen.

2. The excretion of urea and of total nitrogen is said to increase during work; this is, however, not usually the case (Voit), and has never been rigorously proved in a case of sustained labour.

3. The acidity of the urine is said by some to be increased by work (Klüpfel), but this is denied by others (Sawicki, Pavy).

The chemical processes which occur in active muscle are not yet sufficiently apparent; yet, indirectly, there are some points of view which we must examine.

Interdependence of the Phenomena of Muscle, and Theories of Muscular Activity.

No satisfactory explanation of all the phenomena exhibited by muscle as yet exists. The most enigmatical of these phenomena, the diminution in length after stimulation, has hitherto been regarded by most thinkers as a sudden approximation of the smallest particles of the muscle in a longitudinal direction, the ultimate cause of which is a suddenly increased process of combustion. Still no special means of establishing the truth of this surmise has hitherto been possible. When, however, one starts from the numerous analogies which exist between the processes of activity and rigor, one is led to more promising speculations (Hermann).

Analogies between Activity and Rigor.

1. The chemical process during the contraction and rigor of muscle is most probably identical; for (a) given two similar muscles cut out of the body, if one be thrown into rigor directly, but the other only after prolonged exertions, it is found that the total amount of carbonic acid produced in the two cases is the same; it follows that the carbonic acid produced during tetanus and during rigor must spring from the same source. It is actually found that rigor yields so much less carbonic acid the greater the quantity already liberated during tetanus (Hermann). (b) The same holds true in the case of the acid produced; at any rate a muscle which has been severely worked in the body, produces less acid after it is

cut out of the body and become rigid than one which has been inactive (J. Ranke).

2. Both during contraction and during rigor the muscle becomes shorter and thicker, and its elasticity decreases at the same time that its volume diminishes.

3. Heat is generated in both cases.

4. In both acts the muscular contents behave negatively in reference to the unaltered (resting, living) substance.

There occur transitional conditions between contraction and rigor, as the 'idiomuscular contractions' on strong direct stimulation of muscle, and especially of dying muscle; further, the condition induced by stimulating muscles poisoned with veratria or similar muscular poisons; these contractions may continue a longer time, become permanent, and then constitute rigor.

Whilst in former times *rigor mortis* used to be considered as indicating the last flickering of the vital activity, now that the nature of rigor has been recognized it is more correct to compare contraction to a transitory rigor, all of whose characteristics it possesses save only the separation of myosin; yet even the latter process may possibly occur at each contraction, and stand in the same close relation to it as to rigor.

Were myosin to separate as a coagulum in the muscular contents, but dissolve again immediately, we should have no means of discovering it. The connection between contraction and a process of coagulation finds an analogy in the fact that fibrous tissues containing proteids (tendons, nerves, &c.), as well as fresh flakes of fibrin, contract just about the temperature of coagulation in the direction of their fibres (Hermann); a phenomenon which we must confess to be as little explained as is the shortening which occurs during the coagulation of rigor.

Nature of the Chemical Processes in Muscle.

The chemical processes which occur during muscular contraction, no less than during rigor, are independent of a supply of oxygen; for muscle can contract in vacuo or in indifferent gases. Further, as there is no store of oxygen in muscle, the chemical process cannot be one of oxidation, but it is a decomposition associated with the saturation of stronger affinities, so that a conversion of potential into kinetic energy occurs. As products of decomposition there appear carbonic acid, a fixed acid (lactic acid, glycerin-phosphoric acid), and probably also a proteid.

Of the products of decomposition the first two are carried away by the circulation, but the proteid probably not; because the evidences of a consumption of albumin during muscular work are wanting. But not only does the circulation exert a restorative action by removing these waste products, but apparently also by supplying material to take the place of that which has been consumed. It is known that blood carries oxygen to the muscle, especially during its activity; but necessarily an organic substance

must also be supplied with it, otherwise the muscle, giving up carbonic acid and organic acids, would progressively become poorer in carbon.

Hitherto our statements have contained nothing hypothetical. When we try further to conceive how the processes of decomposition and restitution proceed, we enter, however, upon the province of surmises. The simplest conception requires us to assume the existence in muscle of a substance which is, as it were, the substratum of the decompositions; a substance which we may designate the 'energy-yielding' or 'inogen' substance, which necessarily must be highly complex, and which (like hæmoglobin) numbers amongst its products of decomposition a proteid. As, amongst the products of decomposition, myosin remains in muscle, it appears most likely that it is used up again in the process of *restitution*, which may consist in a synthesis associated with oxidation, a synthesis in which the 'inogen' substance is—with the aid of oxygen and an extraneous organic substance (which has been surmised to be glycogen, of which substance the muscle contains a store)—built up again out of myosin. According to this conception myosin would go through a kind of chemical circulation in muscle.

Rigor after arrest of circulation can only depend upon the fact that the process of decomposition is continually proceeding at a slow rate in muscle, comparatively quickly, however, under the influence of heat and in warm-blooded animals; and that when, by a cessation of the process of restitution through the blood, an exhaustion of the supply of materials occurs, rigor follows. The action of stimuli must consist in sudden, almost explosive, accelerations of the process of decomposition. Whilst the muscle is contracting, therefore, its exhaustion is not a far distant probability, and there is therefore a need for increased *restitution*; the acceleration of the blood supply is adapted to effect this purpose. The independence of the CO_2 -producing process of decomposition and the oxygen-consuming process of restitution explains the fluctuations in the quotient $\frac{\text{CO}}{\text{O}_2}$, and accounts for its increase during activity, both for the needs of the muscle and of the whole organism.

The instability of the perpetually decomposing *inogen substance* renders its separation most probably impossible. The greater affinities for oxygen of active or recently active muscle (which in separated muscle may be determined directly by its powers as a reducing agent, Grützner, Gscheidlen) are probably to be ascribed to the products of decomposition. *Fatigue* consists in the process of restitution lagging behind that of decomposition, and it is therefore an alteration which tends towards rigor.

According to the theory which has just been propounded, only non-nitrogenous substances are really used up. This is supported by the observation that the excretion of urea is not increased by muscular exertion (Voit). Attempts have been made to reconcile this observation with the consumption of nitrogenous material; firstly, by the supposition that the consumption of material by muscle was not in general increased during activity, and that therefore the same amount of energy was liberated as when the muscle was at rest, but in another form (Voit); and, secondly, by the theory that the increase in the amount of the material exchanges produced by exertion was counteracted by a corresponding diminution immediately afterwards (J. Ranke). That neither explanation is correct is shown by the fact of the increase in the excretion of CO_2 , both at

the very time of muscular exertion, and during longer periods of work alternated with rest. Since it was first stated that non-nitrogenous substances only were used up during muscular exertion (M. Traube), it has been directly shown that the quantity of albuminous materials used up during the time of exertion, calculated from the urea excreted, is not sufficient, even when an excessive heat of combustion is assumed, to account for the work done (expressed in heat-units) (Fick and Wislicenus, Frankland).

Numerous questions in muscular physiology elude, as yet, all attempts to answer them; as, for instance, the exact explanation of the act of *shortening*—even admitting that it depends upon coagulation—the cause of the immediate disappearance of shortening, the significance of the transverse striation, the relation of the thermic and electrical phenomena to the chemical processes.

The uses of voluntary muscles in the body will be described in the Appendix to this chapter.

The sensory powers of muscle are discussed in Chapter X.

b. Smooth Muscles.

The 'smooth' or 'organic' muscles occasion the less energetic and slower movements of those organs, especially the alimentary viscera, which are not subjected to the influence of the will. They form, for the most part, membraniform expansions of varying thickness (*tunicæ musculosæ*), which are always fibrillated in a definite direction, and often so as to be divisible into layers. These expansions consist of long, spindle-shaped elements, which lie with their longitudinal axes in the direction of the fibrillation. The spindle-shaped elements do not, like the elements of transversely striated muscle, each run the whole length of the fibrillated tract, but they are arranged in rows, end to end. They are regarded as elongated cells which are not known certainly to possess a membrane (sarcolemma), but which contain a somewhat long nucleus. The latter is said by some observers (Frankenhäuser) to be at the same time a nervous end-organ, though others (Schwalbe, Arnold, Hertz) deny this. The cells never exhibit any trace of transverse striation, but there is sometimes an indication of a striation in a longitudinal direction. They are called 'smooth muscular fibres' or 'contractile fibre-cells.'

An examination in polarized light shows that smooth muscular fibres also contain doubly refractive bodies (disdiaclasts), which are not, however, arranged so regularly as in transversely striated muscle, but are scattered throughout the whole mass, so as to give the whole fibre the appearance of being doubly refractive (Brücke). According to more recent theories (Engelmann) the division of the masses of smooth muscle into spindle-shaped elements is considered to be a phenomenon of death, and not to be pre-existent.

The chemical constituents of smooth muscular fibres are apparently the same as those of transversely striated muscle. The existence of a spontaneously coagulable substance may be assumed from the circumstance of the occurrence of death-rigor. As their

reaction is constantly neutral or alkaline (du Bois-Reymond), it cannot be decided whether rigor in this case is accompanied by the formation of an acid; since an acid might be generated in quantity insufficient to overcome the alkali present. The muscles of the contracted uterus are acid to test paper (Siegmund).

The properties of the two classes of muscles are, as far as they have been investigated, almost identical; but the respiration, the chemical changes due to activity, the electrical conditions, the formation of heat, &c. of smooth muscles have not yet been made out. The activity of smooth muscle manifests itself mechanically in the form of a diminution in length, which proceeds according to the same laws as in the case of transversely striated muscle, but at a much slower rate—so much slower that the individual phases (latent period, gradual shortening and re-extending) may be perceived without any assistance; that is to say, after stimulation a considerable time elapses prior to contraction, which takes place very slowly, is maintained for some time at its maximum, and afterwards gradually disappears. Where muscular bands exist (as in the ureter and intestine) contraction caused at one point may be seen to travel like a wave with a velocity of 20–30^{mm} per second, owing, apparently, to the direct conduction of irritation (Engelmann). Automatic contractions have recently been stated to take place in the smooth muscles of the ureter (Engelmann).

Investigations of smooth muscles are very difficult, inasmuch as it is only possible to obtain sufficient material from warm-blooded animals, in which case it quickly loses its irritability.

II. CONTRACTILE CELLS. PROTOPLASMIC MOVEMENTS.

The contractile substance, protoplasm, occurs inclosed in tubular sheaths (in muscle) and also in free, wall-less conglomerations, forming finely granular, and for the most part microscopic, masses of very variable form, and including nuclei. Such contractile masses form the whole substance of the body of many of the lower forms of animal life (*Amœbea*, &c.), or the soft portions of such animals (*Rhizopoda*); colourless blood corpuscles, and the analogous corpuscles of connective tissue, lymph, spleen, mucus, and pus in the higher animals; and the contents of many elementary parts of vegetables (cell-capsules).

All these protoplasmic masses are capable of general and partial contractions. The former follow on stimulation by means of induction-currents. The mass takes on the globular form where it is possible, and where it is not (*e.g.* when the mass is enclosed in a tube) approximates to that form as far as practicable by shortening and thickening (Kühne).

Partial contractions are, however, far commoner, and constitute, perhaps, the only kind which ever occurs in a normal condition. They may produce most manifold changes of form, such, for example, as the protrusion and retraction of processes¹ whereby foreign granules may be dragged into the midst of the mass; movements of the whole structure from place to place, effected by means of the processes (*pseudopods*); movements of the granules, &c. in the interior of the mass; dancing movements (*molecular movements*); the excavation in the interior of the mass of spaces (*vacuoles*) which become filled with fluid. All these forms of movement have been frequently observed (M. Schultze, Brücke, Häkel, Kühne, von Recklinghausen).

Molecular movement has been more exactly studied (Brücke) in the granules of the following cells: colourless blood corpuscles, pus corpuscles, mucous and salivary cells, cartilage cells, and pigment cells of the frog. This form of movement is very generally found. Inasmuch as molecular movement is prevented by many influences which prejudice the life of the cells in which it occurs, and as it always disappears at death, it is clear that this phenomenon is not the same as the molecular movement of inorganic precipitates. The 'cells' above mentioned are not structures possessed of cell-wall and fluid contents, but consist of a tough mass in which, according to certain indications, we must suppose a complicated system of excavations or canals to exist. The matter of the corpuscles when at rest is chiefly aggregated about their nuclei and frequently forms radiating processes towards the periphery. Induction shocks cause the cessation of motion, and afterwards a sudden diminution in the size of the cell with expulsion of granules. Molecular movement is, therefore, a complicated phenomenon, closely connected with the remaining appearances of vitality.

The stimuli by means of which these structures may be induced to activity are the same as in the case of muscle, as are also the conditions of irritability and death (Kühne). At a temperature of 40° C. a species of rigor occurs; a temperature of 36° C. acts as a stimulus producing tetanus (and the globular shape). Deficiency of oxygen destroys the irritability of protoplasmic masses. This circumstance, which is not in agreement with the slight influence which oxygen has on muscles removed from the body, is explained by the relatively greater surface exposed in the case of the small masses.

All protoplasmic structures appear, therefore, to contain the same essential substance as muscle. Its decomposition takes place during conditions of activity, and slowly during repose, until rigor intervenes. Its regeneration is accompanied by an absorption of oxygen at the surface. The weakest acids—even carbonic acid—have a most important prejudicial effect upon all protoplasmic movements.

Certain protoplasmic structures which do not migrate, *e.g.* a portion of the connective-tissue corpuscles of the cornea, are connected with nerve fibres, irritation of which leads to contraction (Kühne, Lipmann, though others doubt it). The great majority

¹ The protrusion of a process can only be explained by supposing contraction to be exerted along the direction of a chord, whereby a segment is pressed outwards. The process becomes long and thin in consequence of the repetition of the contraction along the various chords in the same segment one after another.

are, however, totally independent of the nervous system; and the stimulus which causes the movements is still unknown. These movements may be considered as automatic.

III. CILIATED CELLS AND SPERMATOOZOA.

The superficial cells of the cylindrical epithelium which covers certain surfaces of the body in single or stratified layers are provided at their free ends with fine, structureless hairs or 'cilia' which are constantly in motion. Such surfaces of the body are: the respiratory tract, from the entrance of the nose to the alveoli of the lungs: the female generative organs from the opening of the Fallopian tubes to the os uteri externum: the cerebral ventricles with their communications. In the case of these cilia, no liberation of energy by means of the nervous system takes place so far as is known. Their movements consist for the most part in an alternate bending and straightening; but pendulous, conical, and other forms of motion are said to occur.

Spermatozoa may be regarded as vibratory structures provided with one cilium. The head corresponds to the ciliated cell, and the tail is the cilium. The movement is a lashing to and fro.

If movable particles appear on such a vibratile surface, they are gradually pushed forward in a definite direction. This direction proceeds, in the case of the respiratory and genital apparatus, outwards. In order to explain it we must suppose that the movement of the cilia in one direction takes place more rapidly than in the other, so that one forward push follows another; otherwise, the particles would have regained their old position after each forward and backward swing. The application of this vibratile motion in respiration has been noticed; for its use in the movements of the ovum consult the Fourth Section of the book. Small bodies provided with vibratile cilia, such as many infusorians and spermatozoa, are able to propel themselves actively by means of them through fluids in which they may be placed. The force of the ciliary motion is not unimportant; it is capable of moving in a horizontal direction weights of more than 3 grammes to each square millimetre of surface (Ivymann). In oblique or vertical upward movements each 1 square centimetre can perform in one hour 6·8 gramme-millimetres of work, or the cells can lift their own weight more than 4 metres high (Bowditch).

The circumstances which influence the movements of ciliated cells and spermatozoa are exactly the same as in the case of protoplasm (Roth, Kühne, Engelmann). The conditions necessary to its occurrence are: the maintenance of the state of concentration of the fluid bathing them; the presence of oxygen (Kühne, according to Engelmann they can do without oxygen for long periods of

time); and a medium temperature. Increase of temperature accelerates their motion (Calliburces), as also do variations in electrical currents (Kistiakowsky). Very low or very high temperatures cause a stand-still (cold- and heat-tetanus) which gives place to movement on a return to the normal temperature (Roth). At a temperature of 45° C. a permanent stand-still, *rigor*, is produced, with acidification. Rigor occurs spontaneously after removal from the body. The action of acids is very prejudicial to ciliary movement as well as to the movements of protoplasm. The effect of alkalies in restoring the power of vibration to cilia in which it has spontaneously disappeared (Virchow) merely consists, therefore, in all probability in the neutralization of prejudicial acids (Roth). Other observers, however, ascribe similar reviving powers to acids, alcohol, ether, &c. (Engelmann).

The vibratile movements of ciliated cells and spermatozoa are therefore, most probably, but a special modification of the movements of protoplasmic masses. It is not yet decidedly known whether the cilia are passive and merely moved by the protoplasm of the cell, or whether they also, being themselves of a protoplasmic nature, actively assist.

APPENDIX TO CHAPTER VIII.

THE USES OF MUSCLES.

THE property of muscles to shorten or contract is made use of in the most varied manner in order to bring movable parts towards each other, out of their position of equilibrium, so as to produce changes in the form of the body. The position of equilibrium of the parts of the body is dependent on various mechanical causes, chiefly gravity and tension (elasticity). Changes of form either take place for purposes subject to the will (voluntary movements), or they are brought about by certain mechanisms, which have their seat in the central organs of the nervous system (involuntary movements). The form-change caused by the shortening of a muscle (or of a single muscular fibre, which may be taken as a type of the entire muscle) may be determined in every case, if the position of equilibrium and the degree of mobility of the parts to be moved, and the position of the muscle itself, are known. We have here to consider chiefly two forms of muscular effort. 1. The two terminal points of a muscle are connected together and therefore not movable towards each other. Here a shortening of the muscle can only take place when the muscle does not stretch in a straight line, but between its two points forms a curve. This is the case with the hollow muscular organs, where the muscular fibres run along on a cylindrical, spherical, or otherwise curved surface, either with their

ends joined (directly, or by the juxtaposition of many fibres), or with their ends acting on a body which may be considered fixed (intestine, heart, uterus, bladder, &c.) In this case a tendency to approach a straight line is manifested during the muscular contraction, and hence the surface on contracting exerts a pressure on the fluids which may be contained in these hollow organs. 2. The end-points are movable in reference to one another, being either both movable or (as is commonly the case) one movable and one fixed. In this case the contraction of the muscle, supposing it to be stretched between its two terminal points, causes these end-points and all the parts to which they are fixed to approach each other. In the case in which one of the two points is fixed the other alone will move; if, however, both are movable, then the changes are inversely proportional to the resistances acting in opposition to the movement. The direction of the movement does by no means always lie in the straight line joining the two points. Deviations from this direction are caused: *a*, when the course of the (stretched) muscle or its prolongations (tendons) is not straight, but either curved or bent (when, for instance, the muscle or tendon runs over a pulley-like projection); *b*, when the two fixed points cannot move towards each other in a straight line, their extent of motion being limited by some mechanism or other. In the latter case the whole of the kinetic energy of muscular action (which is determined by the length, section, and degree of activity of the muscle) is not employed in bringing about changes of position, but a part of it is, by the resistance of the mechanism, converted into heat. The part used in changing the form is easily determined by the parallelogram of forces, according to which it is split up into two component parts, the one in the direction of the absolute resistance, the other in the direction of the absolute mobility; the latter of the two components represents the amount of form-change.

Let *ac* and *bc* be two bones which are connected by a hinge-joint *c*, and movable towards each other by the muscle *de*; *ac* being considered fixed, then the point *d* can only be moved in the direction *dg*, vertical to *bc* (the tangent of the arc *di*). The force of muscular contraction is therefore to be resolved into the two components *dg* (the moving portion, or the form-changing portion) and *dh* (the direction of the absolute resistance, or the portion which represents the pressure on the joint). It will be seen at once that as the contraction increases the moving portion, *d₁g₁*, increases, while the other portion, *d₁h₁*, diminishes. If now we call κ the force of traction of the muscle, then that portion of κ which is effective = $\kappa \sin cde$, and the moment in relation to the lever-arm *cd* = $\kappa \cdot cd \cdot \sin cde$; but $cd = \frac{ck}{\sin cde}$; the

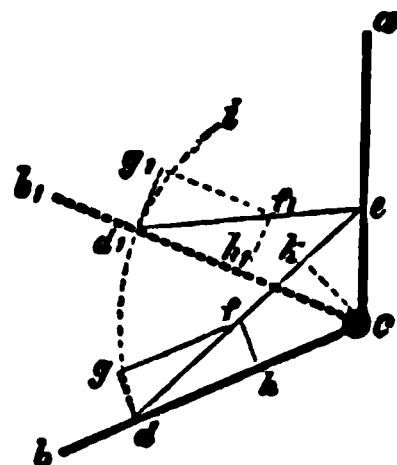


FIG. 26.

moment therefore = $\kappa \cdot ck$; i.e. the muscle acts at every instant as if it acted with its full power on the arm of a lever, the length of which is equal to the shortest distance of the joint from the muscle (Henke).

The conversion into heat of that portion of the work done by the muscle which exerts pressure on the joint is to be taken in the sense that the pressure on the joint increases the friction, whereby the evolution of heat normally due to this cause is increased.

Those muscles which act on rigid parts of the body (bones, cartilage) act almost always as on levers, since the rigid parts are nearly all arranged so as to be movable around a point; hence also the constitution of the momentum of the muscular action as regards weight and velocity will become variously modified. Most of these levers belonging to the second and third kinds, *i.e.* the point of traction of the muscle (power) and the resistance (weight) are on one and the same side of the fulcrum; levers of the first kind are, however, also found, as, for instance, in the forearm, where the triceps acts on the olecranon. The point of traction of the muscle (the power) is generally situated near the fulcrum, and the power-arm is thus much smaller than the weight-arm, and hence only small weights (considered to act at their natural point of application) can be moved, but with great velocity. This arrangement enables us to perform the different movements of the body with great rapidity, and obviates also the clumsy form which our body, particularly the extremities, would have to take under the opposite arrangement, as will be easily understood on reflection.

Where more than one muscle act in different directions on the same part, or where only one muscle acts, the fibres of which, however, have different directions, the resultant can always be easily found by the parallelogram of forces. When different muscles acting on the same part are so arranged that the resulting motion due to the simultaneous action of all becomes $= 0$, that is, the part acted upon remains at rest, then each of these muscles is called the *antagonising muscle* of the rest. The position of equilibrium of any part of the body acted upon by antagonising muscles is, apart from the effect of gravity, that position in which the elastic forces of all muscles balance each other.

We have already spoken of some of the special uses to which muscles are applied in the First Section, particularly when considering circulation, digestion, and respiration. In this chapter we shall consider in a general way the movements of the rigid parts of the body, bones and cartilage, which are so connected with each other as to admit of motion, and then study separately two important groups of motion, namely: 1, the locomotion of the entire body, and 2, those movements in the passage of entrance to the respiratory apparatus which serve for the formation of voice and speech.

Mechanism of the Skeleton.

The elements of the skeleton—the bones—are for the most part movably joined to each other. An exception to this is seen in the connection of the bones by *sutures*, such as are found in the cranial bones, which render the bones absolutely immovable for all such forces as do not endanger the existence of the organism; such bones are then to be considered as forming an immovable mass. Amongst the movable connections of bones we distinguish two kinds: the first of these—the *synchondroses* and *symphyses*—allows but a very slight movement, yet fairly unlimited as regards direction; the combination resulting from this junction is of stable form, to disturb which requires a very strong force, and into which the bones, as soon as that force ceases to act, spring back by virtue of their elasticity. The second kind—the *movable joints*—allows of a free movement without any material resistance, a movement which is, however, limited as regards direction; this form, therefore, has no definite position of equilibrium.

Synchondroses.

The *synchondrosis* is formed by the connection of two opposed, generally congruent, bony surfaces by means of an intermediate more or less solid connecting substance, mostly hyaline or fibro-cartilaginous. Ligamentous sheaths at the place of junction prevent the lateral displacement of this connecting substance. The degree of mobility of this joint depends (1) on the absolute strength of the connection; (2) on its dimensions, for the mobility is (independently of the ligamentous sheath) directly proportional to the *thickness* of the connection, *i.e.* the distance of the two bone surfaces from each other, and inversely proportional to the *transverse diameter* of the connection, *i.e.* the size of the two opposing bone surfaces; (3) on the rigidity of the surrounding ligamentous band. The mobility of these joints is in all cases very small, and muscular traction has therefore scarcely any effect on them; their elasticity is, however, of great importance; especially is this the case with the spinal column, in which we have a series of synchondroses (the intervertebral cartilages) in virtue of which this curved column is endowed with a certain amount of flexibility and great elasticity.

Movable Joints.

In these joints the causes opposed to motion are reduced to a minimum; the direction of the movements is, however, by the form of the joint, limited in various ways. The two bones enter-

ing into a joint oppose to each other smooth surfaces, covered with cartilage (the articular surfaces), which are constantly kept in apposition with each other, over as wide an area as possible, by certain means which will be described presently. The one of the two articular surfaces is always larger than the other.

The most simple joints are those in which the smaller articular surface is always everywhere in contact with the larger. Where this contact is permanent, there can be no other but a gliding movement of the smaller articular surface on the larger; the relative movement of the two bones then depends entirely on the form of the articular surface (as one surface covers the other, the one is the exact cast of the other). In general only certain surfaces of regular form will allow such a gliding movement, and these surfaces are: 1. Plane surfaces (joints of this kind seem not to occur, but the movements which they would allow are: *a.* Rotation of each of the two bones round axes which are perpendicular to the plane of the joint. *b.* Movement of the axis of each bone parallel to itself). 2. Parts of surfaces of rotation, *i.e.* surfaces which may be conceived to have been formed by the rotation of a straight line or of a line of single curvature round an axis lying in the same plane. In this manner, if the rotating line be a straight line parallel to the axis, the articular surface is a cylinder; if it is a straight line, but not parallel to the axis, a cone; if it is a semi-circle and the axis its diameter, a sphere; if it is a segment of a circle and the axis on its convex side, it is a surface of saddle-form; if the axis is on the concave side forming a chord, a cycloid; if it is an ellipse and the axis one of its geometrical axes, an ellipsoid, &c.; lastly, if it is any other curved line, the articular surface is that of some pillar-like, turned body, &c. All joints of this description allow of a rotation of both bones round a common axis, the geometrical axis of the articular surface; they are called *uni-axial* or *hinge-joints* (Ginglymi). An exception to this, however, is presented by those joints whose articular surfaces are parts of a sphere; they allow a rotation around any diameter of the sphere, or, as it is said, round a point, namely, the centre of the sphere; these joints are called *multiaxial* or *ball-and-socket joints* (Enarthrodia). In the *screw-joints* we have a uniaxial joint of peculiar construction. Here the articular surface may be thought to have been formed by the rotating line (which is here a curved line) advancing in the direction of the axis, during the rotation, with a velocity which is proportional to the velocity of rotation. Joints of this description cause an opposite movement of the two articular surfaces around the axis (analogous to the movement of the screw turning within the nut).

The conditions which have just been the subject of consideration are only found in some of the joints of the body, and not even there with mathematical precision. In a great many of the joints

the surfaces are not congruent, and a perfect contact of all the points of the smaller of the two articulating surfaces is therefore impossible. Again, in some of the forms spoken of we notice positions in which the apposition of the surfaces is imperfect; such a condition of things, for instance, enables joints with saddle-shaped or cycloid surfaces to admit of rotation round two axes: to wit, round the axis of rotation and round a second axis which passes through the geometrical centre of the rotating arc and is vertical to the axis of rotation, provided always that the one surface covers only a small part of the other. Wherever the two articulating surfaces are not in contact the spaces are filled up by soft parts or fluids (see below).

Wherever a perfect congruence of the articulating surfaces is not required, the variety of joints and the movements of which they are capable increase beyond measure. It is therefore impossible to draw any conclusions from the mere shape of the two articular surfaces, as to the degree of movement allowed; for the limitation of movements will chiefly depend on the other factors. A general consideration of these irregular joints, whose surfaces are not those of rotation, is therefore impossible; but to consider each one separately would lead us too far.

Mechanism for Maintaining Contact.

The constant and close contact of the two articular surfaces is effected by the following means: 1. The space between the two surfaces is closed, for the ends of both bones are connected by a short tube (the synovial capsule), which is attached round the articular head of each of the two bones; the cavity which is thus formed has only a capillary lumen and is filled with a tenacious lubricating fluid (*Synovia*). The two articulating surfaces can separate no further from each other than the small quantity of synovial fluid will allow, and every further separation is prevented by atmospheric pressure, which presses with a force equal to the product of the surface-capacity of the smaller articular surface and the barometric pressure for the surface-unit. This mode of contact is of importance in joints with large surfaces, especially in the ball-and-socket joints, where any other mode of attachment would restrict the free mobility in all directions. In the hip-joint, the largest ball-and-socket joint of the body, the smaller articular surface (that of the acetabulum) is of such a size, that the atmospheric pressure balances the weight of the whole lower extremity, so that even after all the soft parts surrounding the joint are separated and the synovial capsule cut through, the lower extremity does not drop out of the socket (the brothers Weber); the surface of the acetabulum is further increased, and the closure of the joint ensured, by a thin-edged elastic cartilaginous ring (*Labrum car-*

tilagium) which surrounds everywhere the free margin of the acetabulum and attaches itself closely to the head of the femur in all movements. Where the articular surfaces cover each other but very imperfectly, and the joint-cavity is thus considerably increased, we have the greater part of this cavity filled, not by synovia, but by movable cartilage, masses of fat and ligaments which pass through the joint; the best example of this form is the knee-joint. 2. In nearly all joints ligamentous masses serve to fix the joint; these masses consist either of stretched bands, which run from one bone to the other (in most cases attached to the capsule) or in stretched parts of the capsule itself. As these fixing bands have always to be in a state of tension, they must be so placed as not to hinder movement; with hinge-joints they are therefore always found at both ends of the axis of rotation. In most joints where the surfaces are incongruent (*i.e.* do not cover each other) the axis of rotation is only determined by the insertion of the fixing ligaments. 3. The tension of the surrounding muscles plays an important part in holding the articular ends in apposition.

Check Mechanisms.

The appliances which determine, not the direction, but the *extent* of articular movements, are these: 1. A particular configuration of the *bone*; thus, for instance, the abutting of the olecranon against the sinus maximus of the humerus restricts the extension of the forearm. 2. So-called check-ligaments, *i.e.* ligaments which become stretched in extreme positions of the joints by being so attached that the distance between their two extremes increases to a maximum with the movement of the joint (in joints also where bones restrict the extreme movements we have often ligaments which limit the movement still more). One form in which ligaments which maintain contact act as check ligaments occurs in so-called *spiral joints*, of which the knee-joint forms a good instance. A horizontal section through the articular end of the femur shows as external limit a spiral, the centre of which is situated posteriorly, while its vectors increase in length as they proceed from behind forward. The upper ends of both lateral ligaments are attached to the terminal points of an axis passing transversely across the centre of the spiral (tuberositas condyli interni and externi femoris); the lower end of the internal ligament is attached to the condylus internus tibiæ, that of the external to the head of the fibula. These two ligaments make the knee-joint an imperfect hinge-joint, but inasmuch as with flexion of the knee the smallest vectors of the spiral, and with progressive extension progressively larger vectors, are moved in the direction of the ligaments, so the distance of their points of insertion, and therefore also their tension, increases as the knee passes from flexion into extension, the tension reaching

a maximum beyond which further extension is impossible. This arrangement it is which renders possible the rotation of the fore-leg round its vertical axis independently of the thigh only during flexion of the knee, and not when the lower extremity is extended, in which case the thigh and fore-leg being wedged in at the joint form but one piece. 3. The soft parts also (muscles, tendons, and skin) surrounding the joints, assist by their tension to limit the movements in a manner similar to that of the check-ligaments.

It happens occasionally that when a muscle runs over two joints, the flexion or extension of one of these joints stretches the muscle in such a way as to make it a sort of check-ligament for the other joint: this is called 'passive insufficiency,' in contradistinction to 'active insufficiency,' by which is meant the opposite condition, in which flexion or extension of the one joint slackens the muscle in such a way as to make its contraction have no effect (O. Hüter, Henke).

Conditions of Equilibrium and of active Locomotion of the whole Body.

It will be found convenient for the relations which are to be considered under this head to look upon the body as a chain, with many links and various branches, the joints of which are to be looked for where two bones are movably connected. Such a chain can only be in a stable equilibrium when each joint is sufficiently supported. This will be effected in different ways in the different positions of the body (lying, sitting, &c.) The positions which will be considered here are the erect posture and the sitting posture.

The Erect Posture.

By the free erect posture we mean that position of equilibrium in which the whole body rests entirely supported by the two feet touching the ground. If now the body were a rigid, unjointed pillar, the only condition to be fulfilled would be that the centre of gravity should be supported by the basis or surface of support (which is given by the points of contact between the soles of the feet and the floor), or, in other words, that the line of direction of the centre of gravity should meet the floor within the basis of support. The human body can only be made into such a rigid pillar by having all the movable articulations immovably fixed. In the natural erect posture this is effected almost without any muscular effort, the muscles coming in use only to supplement the somewhat unstable equilibrium.

The articulations to be considered here are the tarsal and tarsal-metatarsal joints, the ankle-joint, the knee-joint, the hip-joint, the articulations of the vertebræ (the symphyses of the pelvic bones may be considered as absolutely fixed) and the articulation between the head and the uppermost cervical vertebræ.

The other articulations (those of thorax, upper extremity and jaw) do not enter into consideration here, for the bones to which they belong are merely appended to, without in any way serving for the support of, the other bones.

1. *The joint between the head and the uppermost cervical vertebrae.*—The two surfaces of the atlas which articulate with the occipital bone form parts of one curved surface with concavity upwards, the curvature of which is slighter antero-posteriorly than laterally. The joint is, therefore, biaxial, *i.e.* the sagittal axis of rotation is situated higher in the head than the frontal, and the greatest amount of motion takes place about the latter. The joint allows also a rotation of the head on the atlas during forward flexion. The most important rotation of the head, however, occurs at the odontoid articulation between atlas and axis. In this joint the odontoid process of the latter vertebra forms a vertical axis of rotation for the atlas and skull. The articular surfaces of the superior oblique processes of the axis are seen, in a sagittal section through atlas and axis, to be convex towards their articular cavities. Therefore, in the mean symmetrical position, the head must be highest, and must glide somewhat downwards, on lateral rotation, like a screw. This arrangement probably guards against torsion of the cord when the head is rotated from side to side. While, in the joints about to be considered, every care seems to be taken to expend as little muscular energy as possible, and to gain the required objects by mechanical means, the great freedom of the axial, atlantic, and occipital articulations requires that the position of the head should be determined by the muscular effort of the numerous muscles attached to it. If this effort is wanting (as, for instance, during sleep), then the head in the erect posture inclines forward and rests with the chin on the chest, for its centre of gravity is in front of its point of support.

2. *The vertebral column.*—The vertebral articulations are chiefly synchondroses; the vertebral column forms therefore a rigid, somewhat flexible and exceedingly elastic rod, variously curved (with the convexity in front in the cervical and lumbar regions, and with the concavity in front in the dorsal and sacral regions). The mobility of the vertebral column, which is quite wanting in the sacral region, increases from below upwards, owing less to the diminished transverse section of the intervertebral cartilages—for this circumstance, otherwise of advantage for movement, is neutralised in its effects by the simultaneous diminution in the thickness of the cartilages—than to the constitution of the true joints between the oblique (articular) processes. In the lumbar region these articular surfaces are nearly vertical, sagittal, and almost parallel (being slightly convergent forwards), so that each upper vertebra is locked in the one below;

rotation about a longitudinal axis is, therefore, quite prevented, while flexion, antero-posterior, or lateral, is possible only in the slightest degree. In the dorsal region the surfaces of articulation of the articular processes are more antero-posterior in aspect, converging posteriorly, and permitting, therefore, a lateral rotation; lateral flexion, also, is not entirely prevented, but antero-posterior movement is quite impossible without a disengagement of articulating surfaces. In the cervical region the articular surfaces become more and more horizontal, and allow of movement in all three directions.

3. *The hip-joint.*—*a.* The centre of gravity of that portion of the body which is to be supported by this joint (head and trunk) is situated near the vertebral column (in front of the tenth dorsal vertebra), in a horizontal plane passing through the xyphoid process (Weber); it will of course vary somewhat with the degree of distension of the digestive canal. A plumb-line let fall from this point (the line of gravity) passes behind the line of junction of the hip-joints, and the trunk would therefore in the erect position fall backwards, but for its attachment anteriorly by the ilio-femoral ligament to the femur (*linea intertrochanterica anterior*). This balancing of the trunk on the heads of the thigh bones might thus be compared to the position of a gun obliquely supported over the shoulder, where the grasp of the butt end by the hand prevents its falling over. The action of the anterior part of the tense fascia lata (*Lig. ilio-tibiale*) and of the stretched *m. extensor quadriceps* is similar to that of the ilio-femoral ligaments, only with this difference, that they are attached to the leg. *b.* The trunk has also to be fixed in a vertical plane to prevent it falling either to the right or left; for as the two feet are not fixed to the floor, a falling over to one side, *i.e.* the rotation of the trunk around the head of the femur laterally, would be possible; this is, however, prevented by the *ligamentum teres*, which checks the adduction of the extended thigh beyond the middle line, and without such adduction, the lateral rotation of the trunk spoken of cannot take place; this is particularly the case in the erect posture, where the *ligamentum teres* is already stretched by the eversion of the thigh and leg (this rotation outwards is due to the action of the *gluteus maximus*);—the external tense sheath of the fascia lata is another accessory to check adduction. *c.* It is unnecessary, as long as the body rests on the two feet, to provide against the rotation of the trunk on the head of the femur; this can, however, be effectually done by the *glutei* and the ligaments.

4. *The knee-joint.*—*a.* The common centre of gravity of head and trunk and thighs is situated somewhat lower than, but not much anteriorly to, the centre of gravity of head and trunk. The line of gravity will therefore here also pass *behind* the point of support of the knee-joint, but the difference is so slight that no

great force is required to prevent falling over (flexion of the knee). The agents are the lig. ilio-tibiale (see above), the slight tension and contraction of the extensor quadriceps, and the lig. ilio-femorale, for in order to flex the knee while the fore-leg is fixed the femur has to rotate outwards, which is prevented by the lig. ilio-femorale. *b.* There is no need of fixing the knee-joint laterally, as this is sufficiently insured by the hingelike nature of the joint (lig. lateralia). *c.* Rotation on the fore-leg during extension is prevented by the crucial ligaments, as described before, p. 310.

5. *The ankle-joint.*—The centre of gravity of the whole body (neglecting the feet) lies approximately in the promontory of the sacrum; the line of gravity will therefore pass a little in front of the line connecting the axes of both ankle-joints, and hence the falling forward of the body has to be provided against. This can be done, *a.*, by the axes of the two ankle-joints forming an angle with each other, so that the simultaneous rotation round both is impossible without a change of position (separation) of the lower extremities; *b.*, by the posterior and smaller part of the pulley-like articulating surface of the astragalus becoming wedged into the fork-like surface formed by the two malleoli, which, when the leg is extended, is so narrow as not to be able to receive the anterior and wider part of the trochlear surface of the astragalus (which would be necessary for the falling forward); this wedging in between the malleoli is brought about by a rotation of the tibia round the fibula, which accompanies the final act of every extension of the leg,¹ whereby the fork-like cavity on the articular surface of tibia and fibula is so turned as to grasp the trochlear surface of the astragalus obliquely. *c.* By the contraction and tension of the flexors of the foot (in the anatomical sense), the muscles attached to the tendo Achillis, tibialis post., peronei post., &c.

6. *The small joints of the foot.*—The tarsal and metatarsal bones form an arch, on the highest point (caput astragali) of which the weight of the body acts, and which rests with three points on the floor, viz. with the tubercle calcanei (heel) and with the capitula of the first and fifth metatarsal bones (the ball of the big and of the little toe). This arch, which the weight of the body tends to flatten, is chiefly maintained by the tension of the ligaments on the plantar side of the foot; only when these ligaments are rendered pathologically lax, does the arch yield (flat foot).

The toes do not serve any purposes for support in the erect posture, but are of use in maintaining the balance, particularly in walking. 'Standing on tip-toe' is likewise only the balancing of the body on the capitula of the metatarsal bones, while the ankle-

¹ This rotation is due to the form of the knee-joint, for which every extension the two condyles of the femur roll forward on the articular surface of the tibia in the manner of a wheel, though not to the same extent.

joint is extended (in the vulgar sense) and the trunk so much arched forward, that its line of gravity falls within the line of support.

The Sitting Posture.

In sitting, the trunk rests on the two tubera ischii like on the rockers of a rocking-horse (H. Meyer), and it can therefore swing forward and backward; we thus distinguish between an anterior and posterior sitting posture, according as the line of gravity falls either in front of or behind the line connecting the two resting points of the tubera ischii. In the anterior sitting posture the trunk is prevented from falling forward, *a*, by supporting it (resting the elbows on the table, &c.); *b*, by fixing it against the lower extremities, by putting the feet on the ground or supporting the thigh on the anterior border of the chair; the fixing is chiefly carried out by the extensors of the thigh. In the posterior sitting posture the trunk must rest against a posterior support, either with the back (high-backed chair) or with the lumbo-sacral region (low-backed chair), but the equilibrium can also be sustained without a support, in which case the point of the sacrum forms the third point of support. Lastly, by stretching the legs forward and fixing the trunk against them by muscular exertion, a position may be found, in which the centre of gravity of the whole is moved forward to such an extent that the feet form the third point of support; when, in this position, the trunk is moved slightly backward, the feet will leave the floor.

Walking. Running.

In walking, the pelvis (and with it the trunk) is rhythmically and alternately supported by one of the two legs (the active leg) and dragged forward a certain distance (the length of a step), while the other (the passive) leg merely hangs on the pelvis. At the commencement of a step the leg which is to be the active leg during this step is placed vertically (slightly flexed, see below), and forms one of the two sides of a rectangular triangle, the hypotenuse of which is formed by the passive leg, stretched out behind and touching the floor only with the toes, while the line joining the feet on the floor forms the third side. The active leg now passes forward carrying the pelvis with it from its vertical position into an oblique (hypotenuse) position, but as the pelvis is to be moved horizontally forward, the active leg must necessarily be lengthened, and this is brought about by the extension of the leg (which we saw at the beginning was slightly flexed) in all its joints: the extension of the foot causes the heel to be lifted from the floor, whereby the point of support also moves to the capitula of the metatarsal bones, but these also are in their turn lifted from the

floor, so that the leg only touches the floor with the extremity of the big toe; the foot is thus as it were raised from the floor like a chain, its separate joints being successively lifted from the floor. The active leg now occupies the same position in relation to the trunk as the passive leg did at the commencement of the step. Now the passive leg, which of course was the active leg of the step immediately preceding, leaves the floor at the commencement of the step and describes a pendulum oscillation forward around its pelvic point of suspension, which brings the foot of the passive leg just as far *in advance* of the active leg as it was *behind* it at the commencement of the step (namely, the length of a step); the foot is now put down and comes to be just vertically under the pelvis, which in the meantime has been carried horizontally forward by the active leg, as we saw. (In order not to touch the floor while swinging forward, the passive leg is somewhat shortened by being flexed.) During the step the active leg has thus passed from its original position (that of one of the two sides) to the position of the hypotenuse of the rectangular triangle, the passive has moved from the hypotenuse position into that of one of the two sides of the triangle; the triangle is moved forward the length of one step; the passive leg has swung forward the length of the step, while the active leg has kept its position; both legs now change their 'part,' that leg which had been the active becomes the passive leg and commences its oscillations, while the passive leg, after being put down on the floor, commences its series of extensions, &c.

The rapidity of walking will therefore depend: 1, on the length of the step; 2, on the duration of the step, which is composed of the duration of the pendulum oscillation and the interval between its termination and the commencement of the next, or, in other words, the length of time during which both feet rest on the floor. 1. The length of step, considered as one of the two sides of the rectangular triangle, is the greater, the greater the difference between the hypotenuse and the other of the two sides of the triangle; therefore, *a*, the smaller, *i.e.* the more flexed the active leg is at the commencement of the step, or the lower the pelvis is carried; *b*, the greater is the difference in length between the leg totally stretched (or totally lifted from the floor) (passive leg) and the leg planted vertically, or, in other words, the longer are the leg and foot—long persons therefore take longer steps than short persons:—2. *a*. The pendulum oscillation is, according to known laws, the quicker the shorter the swinging leg is; the elongation (length of step) is likewise to be taken into account, for the angle of elongation here is relatively large. *b*. The interval of time during which both feet rest on the floor can be shortened at will, and in very quick walking is = 0; the extended foot therefore leaves the floor exactly at the moment in which the other after being swung forward touches it.

A still greater velocity is obtained in the act of *running*, where there is an interval in the period of the step during which both feet are off the ground—the one (the extended) leg has already begun to swing forward before the other has finished its oscillation. The only thing essential here is that the pelvis should swing forward with sufficient velocity, so as to be prevented from falling during the time it is suspended in the air; this is effected by having the active leg at the commencement of the step strongly flexed, and stretching it with great, as it were jerking velocity.

We cannot consider here the different varieties of walking and running and the necessary phenomena thereby observed (W. and E. Weber, H. Meyer), part of which are deducible from what is stated above.

Voice and Speech.

The stream of air which passes through the larynx and the cavities of the pharynx, mouth, and nose during expiration (and in exceptional cases during inspiration also), is made use of in order to throw into vibration portions of those organs and so to produce sounds and noises. To the sounds thus produced the term 'voice' is applied; and both sounds and noises when used as signs for intercommunication are called 'speech.'

1. Voice.

The sounds of the voice are produced by the vibration of the lower vocal cords of the larynx, which are stretched out after the fashion of a membranous tongue in the laryngeal tube. The stream of expired air is projected upon them from below; and the tube into which the vocal cords are fixed—formed below ('wind-pipe') by the bronchial tubes, trachea, and larynx, and above ('sounding pipe') by the larynx, pharynx, buccal and nasal cavities—serves, as is the case in reed instruments, partly to modify the sounds and partly to intensify them.

A *compound tone* (*Klang*) has recently been defined by Helmholtz as any auditory sensation produced by periodically regular vibrations. If the vibrations of the air are simple, like those of a pendulum, a 'tone' is the result. The vibrations producing any complicated regular sound may be resolved by a well-known mathematical law into a number of simple, pendular vibrations, having the ratios one to another of 1:2:3, &c. (Fourier). This resolution of a sound into its elements may be brought about not only mathematically, but also to a certain extent mechanically, in a manner which will presently be described. Every compound tone may therefore be considered to be an aggregate of simple tones, the numbers of whose vibrations are in the ratio of 1:2:3, &c. The deepest of these tones is called the 'prime tone,' and the rest 'harmonics.' If the number of vibrations of the prime tone is n , those corresponding with the harmonics are $2n$ (the octave of the prime tone), $3n$ (the twelfth of the prime tone), $4n$ (the second octave), $5n$ (the compound), &c. The number of the partial tones of a

tone, and their relative intensity, vary much in different musical sounds, as, *e.g.* in the sounds produced by different instruments. It often happens that certain of the harmonics are wanting altogether. A musical sound is named after its most prominent partial tone. If any given tone, say A, occurs as the principal tone in different sounds, the latter are described as A accompanied by differences in 'timbre' or 'quality' (*Klangfarbe*). If the vibration of a compound tone be represented by a curve, the latter will be found to differ considerably in form from that of a simple tone; though it frequently approximates in shape to the wave of its prime tone. Hence it used to be said that two 'tones of different timbre,' of equal pitch and intensity, differed from one another in the characters of their representative curves or waves, which were, of course, of the same height and length in each case.

The resolution of a compound tone into its partial tones is most easily effected by means of resonators (Helmholtz). A simple *tone* is able to throw into sympathetic vibration almost all bodies which have the power of vibrating an equal number of times per second. Hence, any compound tone is capable of calling into vibration neighbouring bodies whose vibratory powers correspond with those of its partial *tones*; and, moreover, of causing them to vibrate with the relative intensity corresponding to the individual tones into which (according to Fourier's law) the sound may be decomposed. If, therefore, a sound with A as the prime tone were produced in the neighbourhood of a series of such resonators or bodies the vibratory powers of which correspond with the harmonics of the tone A, some of the resonators of the series would resound with varying intensities, while others would not sound at all. The simplest resonators are glass or metal globes of a certain pitch, provided with two openings, one of which communicates with one ear of the investigator, while the other ear is stopped. Whenever the tone to which the resonance-globe answers occurs in a sound, it is heard quite loudly by the person whose ear communicates with the globe, while he cannot hear the other partial tones. Just as a compound tone can be analyzed into its partial tones, it is possible in a similar manner to build up a sound from its component parts. The methods of producing and combining simple tones will be explained in the section on speech.

In like manner the sounds produced by the larynx and analogous reed-pipes consist of prime tones and harmonics. The former are very marked, but as many as six or eight harmonics may be detected by the above method of analysis. In the following section, whenever the tones of the larynx and their pitch are spoken of, it must be understood that the *prime tones* are referred to.

Sounds of Reeds and Reed-pipes.

The word 'tongue' or 'reed' is used in acoustics to denote an elastic plate which, when at rest, nearly closes an opening, but which is so arranged that every excursion from the position of rest tends to increase the space between its edge and that of the opening. If a sufficiently powerful blast of air be blown upon the opening, the 'tongue' or 'reed,' as is easily seen, is thrown into vibration. That is to say, the space between the border of the opening and the edge of the plate, while the latter is at rest, is so narrow that the stream of air is not able to pass through it in that condition, but experiences an obstruction. In consequence of this, the air accumulates behind the tongue, and presses upon it with a force which gradually increases until a point is reached at which the elastic plate is forced out of position. This gives a passage to the accumulated air, which rushes through violently, and so reduces the pressure behind the tongue that the latter falls back into its former position; whereupon the whole action is repeated. By this means a continuous stream of air is converted into an intermittent or rather a varying current, and the tongue thrown into vibrations. The sound resulting is really produced by the vibrations of the air (as in the instrument called the Siren) and not by those of the tongue (Helmholtz). The tongue may consist either of a firm elastic plate fixed at one side, as is the

case in many musical reed instruments, or of an elastic membrane (membranous tongue) stretched over the opening. If of the latter kind, the membrane may be so fixed as to leave spaces at both sides, or it may completely cover the opening with the exception of a slit in the centre. The larynx, with its vocal cords and glottis, answers to the last-mentioned description.

The pitch of the note given out by a tongue vibrating under the influence of a current of air (i.e. the number of vibrations per second necessary to produce it) depends upon the time of vibration of the plate itself, as by that is determined the frequency of the impact of the air. The time of vibration of the plate varies inversely as its length and directly as the square root of its elasticity, and therefore, in the case of stretched membranes, directly as the square root of the extending force, just as in the case of an extended string. In the case of membranous tongues, a third influence must be added, viz. that of the violence of the impinging blast of air, which has no effect upon the pitch of notes caused by the vibration of the usual firm tongue. The note is not simply intensified by increasing the strength of the blast, but its pitch is raised (J. Müller). This is explained by the consideration that the tension of the membrane is also at the same time increased, for the middle position, about which the tongue vibrates, deviates further from the position of rest with a strong than with a weak blast; and this greater deviation increases the tension of membranous tongues, as is evident, while it does not affect the elasticity of firm plates, in so far as that property is concerned in the vibrations. The law of this increase in pitch as the blast becomes stronger has not yet been determined. The form and size of the slit *only* affects the note to the extent that, with the same expenditure of energy, the narrower the slit the greater the accumulation of air behind the tongue, the greater the pressure upon the latter, and, in consequence, the stronger the blast it is possible to obtain.

If the tongue is fixed into a pipe (reed-pipe) that portion of it which conveys air to the tongue is called the wind-pipe, while that which is beyond the tongue is called the sound-pipe. In general the effect of the sound-pipe may be said to be to add its own proper tone to the sound produced by the vibrating tongue, and to intensify certain of the component tones of the latter. By intensifying one of the harmonics the pitch of the resulting sound is apparently raised, as the intensified tone becomes prominent as the principal tone. On the contrary, if the primary tone of the sound-pipe is deeper than that produced by the tongue, an apparent diminution of pitch may result. The sound-pipe of the vocal organ has this effect only to a slight extent, the timbre, or sound-colour, of the voice being but slightly, though clearly, modified by it (see below, Vowels), and the principal tone of the sound produced in the larynx remaining the same.

The Larynx.

In the larynx the membranous tongue is formed by two horizontal membranous plates, the *inferior vocal chords*, which extend between the inner surface of the thyroid cartilage and the anterior and external surfaces of the arytaenoid cartilages, and are covered by the laryngeal mucous membrane, which is here provided with pavement epithelium. The slit between them (glottis vocalis) is continuous posteriorly with the interspace between the interior surfaces of the two arytaenoid cartilages (glottis respiratoria). The thyroid and arytaenoid cartilages are so fixed to the cricoid cartilage as to admit of a certain degree of movement. The former, the thyroid cartilage, turns about a horizontal transverse axis in such a manner that its anterior portion approaches or recedes from

the anterior portion of the cricoid. The effect of this movement is to increase or diminish the angle of inclination of the thyroid with the vertical, and, in consequence, to move its superior portion, to which the vocal cords are affixed, forwards or backwards. The arytaenoid cartilages turn principally about their long vertical axes, the effect of which is, as they are pyramids with triangular bases, to cause their edges to occupy different positions, and thus to alter the shape of the slit. From what has been just said it is clear that the thyroid cartilage influences, especially by its position, the length and tension of the vocal chords. The thyroid cartilage may therefore, with regard to the vocal chords, be fitly styled the 'cartilage of extension,' the cricoid the 'basement cartilage,' and the arytaenoid the 'cartilage of position' (Ludwig).

The following are the muscles which govern the relative positions of those cartilages with which the vocal cords are connected:

1. The *crico-thyroidei* approximate the thyroid to the cricoid cartilage, rotating the former about its axis in a forward and downward direction, and thus pulling the upper portion of the cartilage forward, and extending the vocal chords when the arytaenoid cartilages are firmly fixed.

2. The *thyro-arytaenoidei*, which run for the most part within the vocal cords, rotate the thyroid cartilage in a direction upwards and backwards towards the arytaenoid cartilages, and therefore render less tense the vocal cords. Some of their fibres arise from points of the vocal cords themselves, and must therefore, on contraction, confer different degrees of tension upon different parts of the vocal cord: for only that portion will be rendered lax in which the contracting fibres run, while the rest will be kept tense. As, moreover, a portion of the fibres are attached about the external edge of the arytaenoid cartilage, the effect of contraction must be to press together the anterior internal edges (*processus vocales*) of the opposing cartilages, and to separate their posterior internal edges, the result being that the glottis vocalis is narrowed to a small slit, while the glottis respiratoria is increased to a triangular space.

3. The *crico-arytaenoidei postici* drag the external edges of the arytaenoid cartilages, to the lower extremities of which (*processus musculares*) they are attached, backwards and downwards, thus at the same time rotating outwards the anterior internal edges (*processus vocales*), separating them slightly above, and approximating the posterior edges. The effect of this movement is to convert both the glottis vocalis and the glottis respiratoria into triangular spaces, which together form a wide rhombic aperture.

4. The *crico-arytaenoidei laterales* drag the muscular processes of the arytaenoid cartilages downwards, forwards, and outwards, whereby the apices of the two pyramids are somewhat separated one from the other, while the bodies of the latter are so rotated as

to occupy the position they take up on contraction of the thyro-arytænoidei muscles, with the exception that the processus vocales are not so closely applied one to the other.

5. *Arytænoidei proprii* (inter-arytænoidei, transversus et obliqui) approximate the apices of the pyramids and their posterior edges one to the other: If they act in concert with the thyro-arytænoid muscles, both glottis vocalis and glottis respiratoria are closed, and respiration completely interrupted, as, *e.g.* immediately before coughing.

The ventricles of Morgagni give the vocal cords free space in which to vibrate, a provision especially necessary when the vocal chords are much arched by the strength of the impinging blast of air. The superior vocal cords do not appear to play any part in the production of voice. It has certainly been observed that a diminution in the calibre of the sound-pipe above the tongue of a reed instrument raises the pitch of the note produced (J. Müller); but experiment has shown that the excised larynx constantly gives the same note whether the upper vocal cords be present or not. In birds the vocal cords are not, as a rule, concerned in the production of notes, the latter being the function of the 'inferior larynx,' a characteristic organ situated in the majority of cases at the point of division of the trachea.

The larynx receives its supply of motor nerves from the inferior laryngeal branch of the vagus, paralysis of which occasions loss of voice. The superior laryngeal branch of the vagus is considered to supply the crico-thyroid muscle only; but this is denied by some authorities (Nawratil).

Sounds produced by the Vocal Organs.

The general conditions necessary for the production and alteration of sounds will easily be perceived from what has already been said concerning reeds and reed-pipes. In general there is necessary a blast of air of a certain strength, the production of which requires the closure of the glottis respiratoria and the narrowing of the glottis vocalis. These actions are effected by the contraction of the crico-arytænoidei laterales or of the thyro-arytænoidei. During the contraction of the crico-arytænoidei postici the production of voice is impossible. From what has been said above, it is moreover evident that the pitch of the note sounded depends upon the length and tension of the vocal cords, and upon the strength of the blast. It is, on the contrary, independent of the shape of the glottis, which only varies in accordance with the strength of the blast, being narrower in the production of a stronger blast. The pitch is also independent of the form and length of the wind-pipe and sound-pipe in the case of the larynx. It may therefore be stated that the pitch of the note rises: 1. With increasing tension of the vocal cords, which is induced (*a*) by the contraction of the crico-thyroidei (perceptible externally to the touch); (*b*) by the relaxation of the whole of the thyro-arytænoidei; (*c*) by increased violence of blast, of which use is chiefly

made in the production of the highest notes, which can therefore only be rendered *forte* and not *piano*. In order to produce the strongest blast of air through the larynx, the glottis vocalis must be made as narrow as possible, and the glottis respiratoria completely closed, the latter action being effected by the arytenoidei proprii. On the contrary, the tenser the vocal cords the stronger must be the blast of air necessary to cause them to vibrate; and, in consequence, the greater must be the atmospheric pressure in the trachea, as may be proved by means of a manometer fixed into a tracheal fistula (Cagniard-Latour). The pitch of the note also rises (2) according as the length of the portion of the vocal cord set vibrating diminishes. The latter is brought about without at the same time disturbing the tension, (a) by partial contraction of the thyro-arytenoidei; (b) by the close apposition of the processus vocales of the arytenoid cartilages, whereby the portions of the vocal cords in which the cartilages are placed are prevented from vibrating; (c) in larynges of small dimensions, especially in those of women and children, the general range of pitch is higher on account of the shortness of the cords. All the above statements are based upon observations which have, in addition, taught us that as the pitch of the note increases the superior vocal cords approach nearer and nearer to one another without ever completely closing the orifice between them, and that the epiglottis falls more and more over the opening into the larynx (Garcia). Moreover, as the pitch increases the larynx rises; owing partly to the contraction of the elevators of the larynx, and partly, in all probability, to the extension of the trachea under the increasing pressure of the air within. In spite of the apparent simplicity of the arrangements, the process of the production of voice must be extremely complicated. For example, with a given arrangement of the vocal cords any increase in the force of the blast not only intensifies the note but also raises it; as, however, we may require to sustain the same note with a varying intensity (*piano* and *forte*), in order to do so a continual process of compensation must be kept up by the muscles.

In conducting observations on the production of voice in the larynx the following methods are practicable: 1. Palpation and auscultation of the larynx from without. 2. Direct observation of the interior of the larynx by means of a laryngoscope (Garcia, Czermak, Türck). The latter instrument consists of a small mirror, which is held, by means of a handle, at an angle of 45°, over the opening of the larynx and in front of the velum palati, having been previously warmed to prevent the condensation of vapour upon it. Concentrated light is thrown upon this small mirror by means of another concave mirror provided with an aperture to which the eye of the observer is applied. The mouth of the patient is opened wide and the tongue pulled forward. By the arrangement of mirrors the top of the larynx is seen strongly illuminated. 3. Observation of the larynx of a living animal exposed from above. 4. Experiments with the excised larynges of human bodies (J. Müller). The action of the

muscles is imitated by passing threads to which weights are hung over pulleys, and attaching them to the points of insertion of the muscles they are to represent, pulleys and larynx being fixed to a stand. The blast of air is transmitted through a tube fastened into the trachea either from the lungs of the experimenter or from a pair of bellows. In order to measure the pressure of the air in the trachea, a manometer is connected laterally with the tube, which is continuous with the trachea. To study the effect of the sound-pipe, the larynx is left attached to the head. Experiments with the larynges of dead subjects have led to many results inconsistent with the appearances of the living larynx, some of which are still unexplained, and which indicate our lack of knowledge respecting the actions of the latter. 5. Experiments with artificial larynges (J. Müller); to this class of experiments belong, generally, all experiments with reed-pipes.

A greater height of pitch than can be attained by the ordinary method of production of voice is possible by means of the so-called 'falsetto voice.' This is another register, another method of producing voice, which is specially suitable for the higher notes, and which differs from the usual method in a manner which is not yet thoroughly understood. Besides the superior pitch of the 'falsetto notes,' they differ essentially in timbre or tone-colour from those ordinarily produced. It has been observed that the glottis vocalis during the emission of falsetto notes is wider than in the formation of the ordinary voice; and that the superior vocal cords are also farther apart. It is further maintained that the true vocal cords do not vibrate in such an extent of their breadth (in fact only at their edges) in the former case as in the latter (J. Müller, Lehfeldt), owing, according to Mandl, to the partial imposition upon them of the superior vocal cords. Others state exactly the reverse of this, viz. that a greater breadth of the vocal cords is in vibration during the utterance of falsetto notes (Garcia). It is, finally, probable that an extreme tension of the vocal cords is necessary for their production, as is indicated by the sense of exertion in the larynx under those circumstances. Owing to the greater width of the glottis vocalis during the use of falsetto, the air in the lungs is quickly exhausted, in consequence of which it is impossible to sustain a falsetto note as long as an ordinary one. Another distinction between notes of the two registers, and one which depends upon the circumstance last mentioned, originates in the resonance of the wind-pipe and sound-pipe in the two cases; this will be referred to below.

As was said previously, the form and length of the wind and sound-pipes have no influence in the case of the larynx upon the pitch of the notes. They serve, however, to intensify them, and also to modify them, inasmuch as the tones to which they gave origin intensify certain of the harmonics of the voice, and so regulate the timbre, which forms such an essential distinction in the voices of different individuals. By means of voluntary alterations in the form of the sound-pipe the latter may be made to give rise to special tones and noises which are essential to

speech (see below). Owing to the accumulation of mucus, &c. in various parts of the wind-pipe, or about the vocal cords themselves, other noises may be produced, which are unnecessary, or even detrimental to perfect speech. In the production of ordinary voice, resonance is strongest in the wind-pipe, as it contains the air which is being compressed through the narrow slit of the glottis vocalis. The bronchial tubes and the parietes of the chest therefore enter strongly into resonance, and give rise to a trembling motion (*fremitus pectoralis*). Hence, ordinary full and powerful voice is called 'chest-voice.' In the production of falsetto notes, on the contrary, no resonance of the chest takes place, owing to the greater width of the glottis vocalis, the sound-pipe, and the cavities of the nose and mouth being the chief seats of resonance.

The compass of the chest-voice, when the vocal organs are fully developed, ranges from about two to two and a half octaves; but the limits vary with the size of the larynx. The general range of voice is lowest in men and highest in women and children. Thus the bass as a rule extends from E (80 vibrations per second) to f (342); the tenor from c (128) to c'' (512); the alto from f (171) to f'' (684); and the soprano from c' (256) to c''' (1024). The complete compass, therefore, of the human voice ranges from about E (80 vibrations per second) to c''' (1024 vibrations per second), nearly four octaves. The range from c' (256) to f (342) is common to all voices; but the character of the notes varies in different individuals, according to the timbre or 'colour' they acquire from the larynx. In many cases the limits here set down are exceeded.

The development of the larynx bears a definite relationship to that of the sexual powers. At the commencement of puberty there is a sudden increase in its size, and the alto or soprano (treble-voice) of the boy changes into the bass or tenor of the man. This is what is commonly known as the 'breaking' of the voice. In castrated individuals, and in cases of hypospadias, &c., the voice remains abnormally high, higher even than the soprano of women.

2. Speech.

Speech consists of certain tones and sounds which the expired air produces in the cavities above the larynx, and which are used for the purposes of speech, either alone—as in whispering—or in conjunction with the sounds of the voice—as in speaking aloud.

The elements, the sequent arrangement of which constitutes speech, are called *articulate sounds*, and are divided into *vowels* and *consonants*. The distinction, which was formerly described as existing between these two classes, viz. that the consonants are those articulate sounds which cannot be uttered without the aid of vowels, cannot now be held. Both consonants and vowels are now

regarded as being capable of utterance alone, if we except that certain of the former lose somewhat of their characteristics (see below). The true distinction between them is, that the consonants are indefinable sounds, while vowels have rather the character of tones. That is to say, when whispered, the latter are sounds produced in the cavity of the mouth, in which a tone predominates whose pitch may be determined, and when spoken aloud they are modifications of the voice caused by the intensification of individual harmonics by the 'proper' tone of the buccal cavity at the time.

Vowels.

1. In whispering, vowels are produced by expelling a current of air through the cavity of the mouth, the shape of the latter being different for each vowel. Sounds are thus produced in which, by a careful examination, and especially on comparing the various vowels, tones of definite pitch may be distinguished. For the same vowels the same tones are found to be remarkably constant in persons of varying age and sex; and they may be determined by means of the piano (Donders). These tones are the characteristic tones of the cavity through which the current of air passes. They may be still better determined by means of resonators in the following manner. Tuning-forks are set vibrating, and successively placed in front of the mouth, which is arranged as if for the production of a certain vowel; as soon as a tuning-fork is thus placed, the prime tone of which is in unison with that of the buccal cavity, the tone emitted is intensified by resonance, and rendered more audible (Helmholtz). The form of the cavity of the mouth during the production of the vowel sounds U¹ and O, is that of a globular flask with a short neck; during the production of A, that of a funnel with the wide extremity directed forward; of E and I, that of a globular flask with a long narrow neck, &c. Corresponding with the characteristic tones of such bodies, the tones of the cavity of the mouth are:—

for U— <i>f</i>	
„ O— <i>b'</i>	
„ A— <i>b''</i>	
„ E— <i>f</i> and <i>b'''</i>	} one tone for the body of the flask, the other for the neck
„ I— <i>f</i> (?) and <i>d''''</i>	

(Helmholtz). Slight modifications of pronunciation materially affect the tone. The constant occurrence of the same characteristic

¹ The vowel-sounds referred to here are those of the German language :

a	like	a	in	father
e	„	e	„	hen
i	„	i	„	fish
o	„	o	„	open
u	„	oo	„	ooze

tone for the same vowel in buccal cavities of different sizes is accounted for by the proportionate alteration in the orifice of the mouth.

According to more recent researches (König) the characteristic tones of the various vowels are :

for U— b
 „ O— b'
 „ A— b''
 „ E— b'''
 „ I— b''''

The various forms of the buccal cavity are brought about in the following manner. In the production of all the vowels, if the buccal cavity alone is to be used, the passage of the current of air to the nasal cavities is prevented by the raising of the soft palate. If this is not done the vowels have, when spoken aloud, a 'nasal' character. This elevation of the soft palate is least complete during the production of A, becoming more and more so in the case of the other vowels in the following order: E, O, U, I. The various flask-like arrangements of the mouth are thus produced: in A the cavity of the mouth is largest owing to the position of the tongue along the floor, the mouth being wide-open (funnel-shaped). In O and U the globular flask is produced by the elevation of the root of the tongue, and the contraction of the aperture of the mouth into a round opening which is narrower in the case of U than of O. In E, I, the long neck of the flask is produced by approximating the tongue to the hard palate, &c. In sounding all the vowels except U the larynx moves upwards somewhat, least of all in the case of O, and more so in the cases of the others in the following order, A, E, I.

2. In speaking aloud, vowels result from the intensification of various of the harmonics of the voice by means of the resonance of the buccal cavity (Wheatstone, Helmholtz). Hence it follows that vowels may be best sung with those notes which have a prominent harmonic agreeing with the 'proper' tone of the cavity of the mouth; further, that the individual vowel-sounds are not distinguished by the peculiar arrangement of the intensified harmonics, but by their absolute height.

The vowel-sounds may easily be analysed by means of the resonance-apparatus mentioned on p. 318. The analysis is more exact if made by means of a phonautograph (Donders), in which a tense membrane is allowed to take up the vibrations of a particular vowel-sound and to trace them upon a rotating cylinder. In order to reproduce a vowel-sound synthetically, all that is necessary is to raise the damper from the strings of a piano and to sing the vowel in a clear, loud voice in front of the instrument. Under such circumstances all the strings the tones of which exist in the vowel-sound as harmonics, are called into vibration, and to a degree of intensity corresponding with the intensity of the harmonics. The vowel, therefore, *resounds* from the instrument, not simply as tone, but as a vowel (Helmholtz). The direct synthesis out of simple tones is still more instructive. A number of tuning-forks corresponding in pitch

with the various harmonics of a primary tone (*e.g.* B, *b*, *f*, *b'*, *d''*, *f'*, *as''*, *b''*, *d'''*, *as'''*, *f'''*, *b'''*) are set vibrating by means of electro-magnets, which are so arranged that the current passing round them is opened and closed by the vibrations of a special tuning-fork fitted up on the principle of Wagner's hammer. The tones of the tuning-forks are rendered inaudible by placing them upon caoutchouc. Before each fork, however, stands a resonance-tube tuned to the prime tone of the fork. When the tube is open, it renders audible the prime tone of the tuning-fork—a simple tone, therefore. With this apparatus it is possible, by opening the resonance-tube more or less perfectly by means of keys, to sound and combine at will strong or weak individual tones. In this way not only vowels, but also the characteristic sounds of various instruments, may be synthetically represented. The same result may more simply be effected by means of reed-pipes, which yield simple tones (Helmholtz).

Diphthongs are produced during the transition from the form of mouth necessary for the one vowel to that necessary for the other. They consist of two sounds following quickly one upon the other.

Consonants.

The articulate sounds called consonants are sounds produced by the vibrations of certain easily moveable portions of the throat and mouth; and they have a different sound according as they are accompanied by voice or not. The pharyngo-buccal canal is capable of constriction or interruption at three places, at each of which vibrations may be produced; these are: 1. At the lips, the constriction being formed by the two lips, or by the upper (or lower) lip with the lower (or upper) row of teeth. 2. Between the tongue and the palate, the constriction being brought about by the apposition of the tip of the tongue to the anterior portion of the hard palate, or the posterior surface of the upper row of teeth. 3. At the fauces, the constriction being due to the approximation of the root of the tongue and the soft palate. Sounds may originate at each of these places of interruption; and hence consonants may be classified into three series, viz. labial, dental, and guttural consonants.

The sounds which may be formed at each of the places of interruption are (Brücke):

1. **EXPLOSIVES.** These are produced by suddenly opening or closing the passage at one of the points mentioned during the expulsion of air: *a*, without the aid of voice, P, T, K; *b*, with the aid of voice, B, D, G.

Opening of the passage is necessary for the formation of one of these consonants when it begins a syllable; closure when it ends one (*e.g.* *pa*, *ap*). As P, T, and K are distinguishable from B, D, and G respectively only by the absence or presence of the voice, no sharp distinction is possible between them during whispering.

2. **ASPIRATES.** The passage is constricted at one of the above-mentioned points to a small slit through which the current of expired (or inspired) air can rush. Hence arise the following consonants: *a*, without the aid of voice, F, S (sharp), Ch (guttural),

b, with the aid of voice, *V*, *Z*, *J* (as in the German *ja*, &c.) At the constriction between the tongue and the palate a second aspirate may be formed, in addition to the sharp *S*, viz. *L*, by completely closing the passage in front and allowing the air to escape only at the sides between the molar teeth. By forcing air through two narrow spaces situated one behind the other, viz. that between the tip of the tongue and the hard palate, and that between the two rows of teeth, two other sounds may be produced: *a*, without the aid of the voice, *Sh*; *b*, with the aid of the voice, *Zh*. If a space be left between the tip of the tongue and both rows of teeth, the following consonant-sounds are produced: *a*, without the aid of the voice, *Th* (hard) as in *than*; with the aid of the voice, *Th* (soft) as in *thunder*. The guttural *Ch* may be produced near the front of the mouth, as in the German word, *ich*; or near the back, as in *ach*.

F and *V*, &c. are distinguished in the same way as *P* and *B*, &c.

3. **RESONANTS.** The current of air no longer passes through the usual opening, which is closed, but through the nose, which is left open by the depending soft palate. The aid of the voice is necessary. The consonants thus produced are *M*, *N*.

4. **VIBRATORY SOUNDS.** There are three varieties of the vibratory *R* which differ in their place of origin. The first is the labial *R*, produced by the vibration of the lips, which does not occur as an articulate sound in any European language; the second is that produced by the vibration of the tip of the tongue in the constricted portion of the buccal cavity formed by the tongue and the teeth; and the third is the guttural *R*. In order to produce them the pharyngo-buccal cavity is constricted at the necessary point, but not firmly; and the margins are then set vibrating by the expiration of air. The vibrations are, however, too slow to give forth a definite note.

The consonants may therefore be grouped in the following manner:

	Labials	Dentals	Gutturals
1. Explosives:			
<i>a</i> . Without the voice . . . }	<i>P</i>	<i>T</i>	<i>K</i>
<i>b</i> . With the voice	<i>B</i>	<i>D</i>	<i>G</i>
2. Aspirates:			
<i>a</i> . Without the voice . . . }	<i>F</i>	<i>S</i> (hard), <i>L</i> , <i>Sh</i> , <i>Th</i> (hard)	<i>Ch</i> (in 'ich' and 'ach')
<i>b</i> . With the voice	<i>V</i>	<i>Z</i> , <i>L</i> , <i>Zh</i> , <i>Th</i> (soft)	<i>J</i> (in 'ja')
3. Resonants:	<i>M</i>	<i>N</i>	<i>N</i> (nasal)
4. Vibratory sounds . . . }	Labial <i>R</i>	Lingual <i>R</i>	Guttural <i>R</i>

H is the sound produced in the larynx by the quick rushing of the current of air through the widely opened glottis.

Compound consonants are produced by suddenly opening the air-passage previously closed for the utterance of P, T, or K, as the case might be, and allowing the current of air to rush through the second of the before-mentioned places of constriction narrowed as if for the utterance of S (hard): thus are produced Ps (Greek Ψ), Ts (German Z), and Ks (X). Other compound consonants are formed by the rapid transition from the position of mouth necessary to produce one consonant to that necessary to produce the other.

Observations upon the movements which take place during the formation of speech are made partly by direct inspection of the cavity of the mouth while the latter is open, and partly by palpation by means of the fingers introduced into the mouth. In order to decide whether the posterior nares are opened or closed at any particular time, a candle-flame, or a bright, cold mirror may be placed in front of the nasal openings on the face. Finally, many of the conditions of speech have been determined by noticing the mode of utterance in persons suffering from pathological malformations of the vocal organs; such as absence, or adhesion of the soft palate, &c.



PART III.

THE 'LIBERATING' OR 'DISCHARGING' APPARATUS.

The Nervous System.

THE nervous system, the importance and general relations of which have already been referred to in the Introduction, comprehends three distinct orders of apparatus, which may be classified as consisting of (1) purely conducting organs, (2) terminal end-organs, (3) central organs.

CHAPTER IX.

THE CONDUCTING APPARATUS (NERVES).

A. GENERAL PHYSIOLOGY OF NERVES.

THE elements of a nervous cord are thin, longitudinally striated fibres, which are arranged side by side into round or flattened bundles (*nerves*), and bound together, like the 'muscle tubes' of muscle, by means of interspersed connective tissue which extends over the exterior of the bundle as a firm fibrous sheath (*perineurium*). Each nerve-fibre is a tube filled with partly fluid contents. The thin walls of the tube (the primitive sheath, *neurilemma*) consist of an elastic membrane like the sarcolemma of muscles, and are provided with large nuclei. The contents of the tubes are divided into a thin cord running in the axis—the *axis-cylinder*—and a shining mass surrounding it—the *medulla or medullary sheath*—composed of a substance which easily breaks up.

The fine nerve-fibres of a certain class do not possess a medullary sheath, and consist simply of an axis-cylinder and a sheath (*non-medullated nerve-fibres*). A third class of nerve-fibres is characterized by the regular varicose arrangement of the axis-cylinder, and the absence of all signs of a sheath (*gray or varicose fibres; fibres of Remak*).

The distribution of the various classes of nerve-fibres will be discussed in Chap. XI.

The axis-cylinder is especially well seen after the death of the nerve; and it has therefore been considered by many to be a post-mortem (contracted) coagulum. The greater number of observers, however, regard it as existing during life; and, indeed, it must be considered to be the most important element of the nerve-tube, as it is connected directly with the essential portions of the central and peripheral nervous end-organs, unless we are prepared to regard the latter also as the appearances of coagulation. Many axis-cylinders, if not all, consist of a bundle of very fine 'nervous fibrillæ' (Max Schultze). An especially delicate species of axis-cylinders (simple nerve-fibrillæ, Max Schultze) is discovered in the central nervous organs, forming there intercentral connections between the ganglion-cells (Chap. XI.); the thickness of a nerve-fibre depends essentially upon the greater or less thickness of the medullary sheath, which seems to serve the purpose of nourishing the axis-cylinder. Under certain methods of treatment medullated nerve-fibres exhibit at definite distances apart annular constrictions at which the medullary sheath is said to be interrupted. As a nucleus of the neurilemma is constantly found between two such constrictions, it would

seem as if the appearances were indications of the original formation of a nerve-fibre out of a row of cells, the constrictions corresponding with the divisions between the primitive cells (Ranvier¹).

Digestion dissolves nerve-fibres, leaving, however, in the case of medullated fibres, a horny residue which essentially consists of two concentric layers, between which the medullary sheath appears to extend (Ewald and Kühne²).

Chemical Constituents of Nerves.

Scarcely anything is known about the chemical constitution of nerves. The axis-cylinder seems to be related in its characters to the albuminous bodies. The medullary sheath, whose appearance and behaviour towards solvents indicate a fatty nature, possibly contains no proper fat, but only lecithin and its compounds. These, however, have only been prepared hitherto from brain-substance, &c., and not from nerve-fibres themselves. Nerve-fibres contain in addition cholesterin and creatine, besides the ordinary constituents of connective tissue and a horny substance (neurokeratin).

The reaction of fresh nerve in a state of rest is neutral (Funke³). The reaction and composition of brain-substance will be discussed in Chap. XI.

The Various Conditions under which Nerves exist.

Nerves, like muscles, present themselves under three conditions: 1. The usual condition of Rest. 2. The condition which terminates in Death. 3. The condition of Activity. The three conditions cannot, however, in the case of nerves, be distinguished by mere inspection, as the physical properties of the nerves undergo no alteration.

The mere mechanical properties of nerves have, as a rule, no interest physiologically speaking. Flaccid nerves have a tendency to form fine transverse folds—the transverse striæ of Fontana.

Nerve in a State of Rest.

A certain amount of material exchange occurs in nerves in a state of repose, just as was seen to be the case in muscles, although hitherto neither absorption of oxygen nor formation of carbonic acid has been proved to take place. The existence of such processes may, however, be inferred from the fact that nerves contain specific tissue-elements which differ from the constituents of the blood. The extent of the material exchanges occurring in nerves must be very slight, as nerves are almost destitute of blood vessels; but nothing more particular is known about them.

¹ Ranvier, *Archives de Physiologie*. 1872, p. 129.

² Ewald u. Kühne. 'Ueber einen neuen Bestandtheil des Nervensystems.' *Verhandl. des naturhist. med. Verein zu Heidelberg*. 1 Bd. 5 Heft.

³ Funke, *Centralblatt*. 1869, p. 721.

The Process of Death in Nerve.

The process of death of nerve-tissue is not marked, like that of muscle, by any evident process of coagulation ; it is only recognized by the loss of irritability (see below), the appearance of an acid reaction (Funke), and the electro-motor phenomena which will be described hereafter. Dead nerve-tissue undergoes putrefaction, just like dead muscle, if not prevented from doing so by a process of drying.

Nerve in a State of Activity.

The active condition is induced in nerves by the same means as in muscles, viz. by some liberating force—some stimulus ; and the term ‘irritability’ is applied to nerves as to muscles, to indicate this property of being called into activity by the application of a stimulus. ‘Excitability’ is the term often employed to distinguish the irritability of nerves.

The conditions of irritability and the stimuli, in the case of nerves, agree in many particulars with those of muscles. The irritability of nerves is greater than that of muscles ; that is to say, stimuli which are physically equal (*e.g.* equal degrees of variation in electric currents which are of the same intensity), have a more powerful stimulating effect when acting upon muscle through a nerve, than when acting directly upon a muscle deprived of its nervous connections by the action of curare (Rosenthal).

Excitability.

1. Excitability is connected with the normal constitution of nerves. Considerable modifications of the chemical composition (as loss of water by drying, the action of caustics, &c.) abolish excitability.
2. Any decided mechanical alteration in the condition of a nerve, such as tearing or twisting, destroys its excitability.
3. When a nerve ceases to be connected with a living *central organ*, owing, for example, to section of the nerve or death of the central organ, its irritability increases considerably at first, but afterwards diminishes and finally disappears. Transverse section of the nerve hastens the process (Rosenthal) ; which, moreover, takes place more quickly in the central portions of the nerve than in those nearer the periphery (Ritter and Valli's law). A nerve separated from its central organ, but still allowed to remain in the body, subsequently undergoes certain chemical and morphological changes, denominated ‘fatty degeneration.’ If, however, the cut ends be kept in apposition, they grow together after some time. The presence of oxygen

is as little necessary to the maintenance of irritability in the case of excised nerves as in that of muscles (Pflüger and Ewald).

4. Continued repose of a nerve diminishes and destroys its irritability, and leads at last to fatty degeneration. Sensory nerves, when cut across, undergo degeneration in both their central and peripheral portions—in the former because they can no longer be irritated, in the latter because they are separated from the central nervous organ.
5. Continued activity of a nerve diminishes its excitability in proportion to the time, and may destroy it altogether (Exhaustion). In the former case rest restores the nerve to its original condition. The alterations which take place in nerves during exhaustion have not yet been made out.
6. The effects of temperature, hitherto studied only on frogs, are the following: Temperatures above 45° C. destroy excitability the more rapidly the higher they are, the destruction being instantaneous at 70°. If the temperature to which the nerve has been subjected have not exceeded 50°, excitability may be restored on cooling (Rosenthal). Below 45°, a rise in temperature at first increases, but afterwards diminishes, irritability; the increase being greater and the diminution more rapid according as the temperature is higher. Rise in temperature, therefore, diminishes the duration, while it increases the intensity, of excitability (Afanasieff). A sudden rise of temperature to 35°–45° acts as a stimulus (see below).
7. The effects of electrical currents through nerves appear to be especially important. If a constant galvanic current be passed through a portion of a nerve, its whole length enters into an altered condition (du Bois-Reymond¹), in which, among other circumstances, its power of being stimulated is modified (Eckhard, Pflüger²). This is called the '*electrotonic*' condition, or '*electrotonus*' (du Bois-Reymond). The condition which obtains in the region of the positive electrode (the *anode*) is called '*anelectrotonus*,' and that in the region of the negative electrode (the *cathode*), '*catelectrotonus*' (Pflüger). The constant current which causes this change of condition is called the '*polarising*' or '*electrotonising*' current. The boundary between the anelectrotonic and catelectrotonic states, called the '*indifferent point*' of the '*intrapolar region*,' is situated near to the anode when the polarising current is weak, and moves towards the cathode as the polarising current increases in strength. The influence of electrotonus is strongest in the neighbourhood of the pole.

¹ Du Bois-Reymond. *Von der Veränderung des Nervenstroms durch einen stetig einwirkenden elektrischen Strom, oder den elektrotonischen Zustände der Nerven, Untersuchungen*. Vol. ii. p. 289.

² Pflüger, *Untersuchungen über die Physiologie des Electrotonus*.

Excitability is *increased* in the *catelectrotonic area* and *diminished* in the *anelectrotonic area*. Immediately after the cessation of the polarising current the conditions of excitability become reversed in the different regions (excitability being increased near the anode and diminished near the cathode); but afterwards they gradually regain the normal (Pflüger). At the instant of closure of the current, excitability is said to be increased in the whole nerve (Wundt). (Reference should be made in this connection to what is said below about Stimuli and the Electrical Phenomena of Nerves.)

The variations of excitability may be explained, for the sake of illustration, by supposing for the moment that the particles of nerve-matter in the anelectrotonic area have a diminished, while those in the catelectrotonic area have an increased, degree of mobility. Variations of excitability are measured either by differences in the degree of contraction produced by stimuli which should be weak; or by variations in the strength of the stimulus, which is just sufficient to induce the slightest contraction. The results so obtained admit of an explanation, to be mentioned below, which does not require the assumption of variation in the degree of excitability.

The electrotonic variations of excitability may be demonstrated in the case of man also by the application of a constant current (Eulenburg, Erb). To prevent disappointment, however, the test-stimulus must be applied at the points where the current is most dense, as it is only in the immediate neighbourhood of the electrodes that the current passed through the nerve is dense enough to induce the phenomena of electrotonus; and hence it is that it appears as if there were an anode on each side of the cathode, and a cathode on each side of the anode (Erb).

8. In the same nerve all fibres do not possess the same excitability, as measured by the effects produced on muscles by their irritation. In the sciatic nerve of the frog, for instance, the weakest stimuli induce flexion, the stronger extension of the foot (Ritter, Rollett).

Stimuli.

The stimuli which are able to call a nerve into activity are the following:—

1. *Variations in an electrical current.*—A perfectly constant current flowing through a nerve does not appear to be essentially capable of stimulating the nerve to activity, even if apparently so. Every variation, on the contrary, in the intensity of the current (or, more exactly, in the density¹ of the current) produces irritation in the nerve, which is more powerful the more quickly or suddenly

¹ Whereas the external effects induced by a current in passing through a conductor, such as its effect in causing deflection of a magnet, merely depend upon the *intensity* of the current, the internal effects, such as the heating of the conductor, depend upon the relation of the section of the conductor to the intensity; the internal effects depending upon the '*density*' of the current, by which is understood the intensity divided by the area of the transverse section of the conductor through which it is flowing. In nerves, as compared with muscles, the electro-motive force being the same, the '*intensity*' (in consequence of the great resistance occasioned by their thinness), is very small; the *density* of the current is however almost as great as in muscles.

the variation occurs (du Bois-Reymond). The variation which is most frequently used as a stimulus is that produced on making or breaking a current through the nerve: *i.e.* the passage of the intensity from nought to the full strength of which the current is capable, or the reverse. Any other variation, however, acts as a stimulus; *e.g.* the sudden increase or diminution in strength of a current already passing through the nerve; or the mere alteration of the density of the current in a nerve, the intensity of the whole current remaining unaltered.

If the time occupied by one complete variation be supposed to be divided up into fractions, and these fractions taken as abscissæ: and if the density of current corresponding with each of those fractions of time be regarded as ordinates; a curve will be obtained which will represent the course of the variation according to time. From the law just enunciated of the stimulation of nerves by currents, it follows that the value of a given variation as a stimulus is greater the more sudden the ascent or descent of this curve; but the more exact conditions of this relation are at present unknown. From the same law we gather that a nerve may be very powerfully stimulated by means of a very weak current, if only the rapidity with which it is allowed to break into or out of the nerve be sufficiently great. Hence the shocks of frictional electricity have a very powerful stimulating effect; for although the amount of electricity really present is very small, the currents it forms are extremely rapid in their appearance and disappearance. For similar reasons, the rapid currents of the induction coil are generally used for the purposes of stimulation. On the other hand, it is evident that a very strong current may be made to pass through a nerve without inducing excitation, if care be taken to do it extremely gradually.

The above-mentioned stimulation by *constant* currents is evidenced in the case of motor nerves by the induction of tetanus in the muscle with which they are connected, and in the case of sensory nerves by sensations (pain, &c.), which continue during the passage of the current. The appearances in the former case are more marked with ascending than with descending currents. They are present in the case of very weak currents, and become more and more decided as the current increases in strength, until a certain limit is reached, above which the electrotonic modifications of the conditions of irritability again render the results less marked (Pflüger).

The stimulating effect of a current operates, on *closing* (and, in general, on any *positive* variation), at the *cathode* only; and, on opening (*negative* variation), at the *anode* only. In other words, *a portion of nerve is stimulated by a current, when the latter causes in it the appearance (or increase) of catelectrotonus, or the disappearance (or diminution) of anelectrotonus* (Pflüger). The stimulation of the other portions of the nerve is only a consequence of the transmission of excitation (see below).

Expressed in the hypothetical manner, Pflüger's law of stimulation would run thus: The passage of the molecules of nerve-matter from the usual into the mobile (catelectrotonic) condition; or from the hardly mobile (anelectrotonic) into the usual condition, acts as a stimulus. On the contrary, the passage from the usual into the hardly mobile (anelectrotonic) condition; or from the easily mobile (catelectrotonic) into the usual condition, does not act as a stimulus. In this form the law is somewhat more intelligible, on account of the rationale supplied.

The experiments from which this law has been deduced are rather compli-

cated. As they have been for the most part made upon mo'or nerves, the law is also called the 'Law of Contraction.' If the stimulating current be allowed to pass through a given (central) portion of the nerve, the whole of the latter is divided into two parts, in which opposite conditions obtain, in one the *anelectrotonic*, in the other the *catelectrotonic*. The above law affirms that, on closing the stimulating current, it is the catelectrotonic area only, while, on opening, it is the anelectrotonic area only, which suffers stimulation. Hence we may, if we like, express the law as follows: *Stimulation proceeds from the cathode on closing, and from the anode on opening, the stimulating current.* If the stimulating current has an *ascending* direction (i.e. if the positive electrode is nearer the muscle) it is evident that the upper portion of the nerve will be stimulated during closure, and the lower during opening, of the stimulating current: and the contrary results will obtain if the current is *descending*. It may now be asked, which regions of the nerve, on stimulation, call the connected muscle into activity, i.e. induce contraction; and the answer will be found to depend upon the strength of the current used in stimulation. Thus, when the current is strong, the anelectrotonic area loses its powers of conductivity (see below), in consequence of which only the stimuli operating in the portion of nerve between it and the muscle can possibly produce a contraction. In the case of strong currents, therefore, the *descending* current can only act effectively on closing and the *ascending* only on opening. With currents of medium strength both areas or regions have the power of inducing stimulation and causing contraction of the connected muscle, as the conductivity of the whole nerve is nowhere interrupted. In this case, therefore, whatever the direction of the current, contraction will follow on both opening and closing. With currents of the weakest sort, that area only will act as a stimulus in inducing contraction which is most favourably situated for the purposes of stimulation; that is to say, *ceteris paribus*, that area which is most removed from the muscle (see under Conductivity). When, therefore, the current is very weak, closing the ascending, and opening the descending, current should induce contraction. But, as the appearance of catelectrotonus is a stronger stimulus than the disappearance of anelectrotonus, the latter operation, viz. opening the descending current, gives place to closure of the same as a more powerful means of stimulation; and, in consequence, the weakest descending currents do not give opening—but closing—contractions. The law of contraction may be formulated thus:

(R = Rest, C = Contraction).

Strength of Current	Ascending		Descending	
	On closing	On opening	On closing	On opening
Strong . . .	R	C	C	R
Moderate . . .	C	C	C	C
Weak . . .	O	R	C	R

Induction currents are currents which are called into existence very suddenly and disappear somewhat more slowly. Of the two means of stimulation which follow thus immediately one upon the other, the former, according to the above-mentioned general law of stimulation, is the more powerful. In the case of weak currents, indeed, it is the only one of the two which is effectual; so that weak induction currents act in stimulation like the closure of a similarly directed constant current. With this understanding, the Law of Contraction holds for induction-currents also (Rosenthal).

The effects of stimuli on the centripetal nerves of animals can only be imperfectly investigated. The method adopted is to induce an extreme reflex

irritability by means of strychnia-poisoning, in order that peripheral stimuli may readily induce tetanic muscular contractions (Chap. XI.) An analogous law of stimulation may be demonstrated in the case of inhibitory nerves, as, for example, the inhibitory fibres of the vagus (Donders).

If the current used in stimulation is very strong, or has been kept closed for some time, tetanus occurs on opening (tetanus of Ritter), instead of the usual single contraction.¹ This tetanus immediately disappears on reclosing the same current, but is, on the contrary, intensified if the current is first reversed and then closed. As Ritter's tetanus results from the strong irritating effect due to the disappearance of anelectrotonus, it ceases immediately on separating the anelectrotonic area of the nerve from the muscle; which can only be done, for obvious reasons, in the case of descending currents, where section of the nerve at the 'indifferent point' accomplishes the purpose (Pflüger). The condition of the nerves just referred to was formerly considered to be a distinct modification of excitability, similar to those described on p. 336; and it used to be said that the constant current increased the excitability of the nerve for the opening of a current in the same and for the closure of a current in the contrary direction; and *vice versâ* (Rosenthal). The phenomena described are, however, easily explicable by Pflüger's law of stimulation. If the stimulating current is too weak, or has been closed for an insufficient time, or if the excitability of the nerve is diminishing on account of the approaching death of the latter, then a somewhat languid contraction takes place, followed finally by the usual opening contraction, instead of the tetanus of Ritter.

The power of constant currents to restore irritability to exhausted muscles, also belongs to this category of phenomena; for it must not be forgotten, that all the laws of the electrical stimulation of nerves are equally applicable to muscles. In the case of muscles also, for instance, stimulation only results on opening a current in the same, or on closing a current in the contrary direction.

As stimulation, according to Pflüger's law, depends upon the appearance or disappearance of a different condition (electrotonus) of the nerve, none can result from currents which are too transitory to allow of the completion of the electrotonic state. Experiment confirms this statement; as currents which do not last more than 0.0015 of a second are incapable of stimulating nerves (König).

Currents have the most powerfully stimulating effects when they traverse the nerves in the direction of their length, being indeed powerless in this respect when flowing transversely. Currents in directions intermediate between these two extreme positions have intermediate values as stimuli, the laws of which have not yet been established. The length of the portion of nerve traversed by the stimulating current, which was formerly supposed to influence irritability favourably, is now known to do so only in the case of descending currents, while in ascending currents the shorter the piece of nerve included between the electrodes, the better appears to be the stimulating effect. Stimulation, therefore, according to the law of electrotonus, is more powerful the nearer the cathode to, and the farther the anode from, the muscle (Willy).

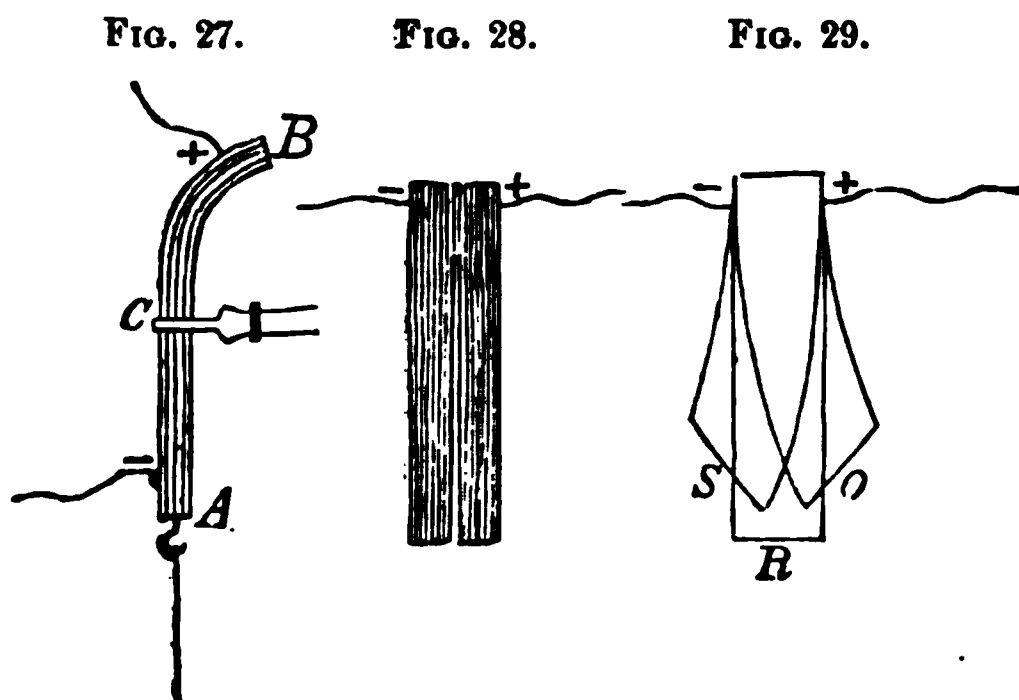
In the electrical stimulation of muscles, the same laws hold as in that of nerves. Here, also, it is only variations in currents

¹ See du Bois-Reymond, who first employed the expression 'Ritter's tetanus,' *Untersuchungen*. Vol. i. p. 865.

that produce stimulation, which, as before, proceeds, on closing, from the cathode, and, on opening, from the anode (von Bezold). As changes take place more slowly in muscle than in nerve (as evidenced, for example, by the different degrees of rapidity with which they transmit impressions), length of duration of the stimulating current is more necessary in the former than in the latter for the production of stimulation. Hence all induction-currents, and the more transitory constant currents, are unable to stimulate to contraction muscle deprived of its nervous connections by curare, while they are able to cause contractions in a muscle by acting upon its motor nerves (Brücke). This fact was early known to be the case with muscles, the nervous organs of which were rendered incapable of performing their functions by exhaustion, local death, pathological paralysis, &c. (von Bezold, Fick, Neumann).

Pflüger's law of stimulation may be demonstrated to hold in the case of muscles in the following ways (Engelmann):—

1. A muscle A B (fig. 27) is fixed by its middle portion C, care being taken not to crush it, and the lower half is arranged so as to register its contractions



on a myographion. If the cathode be placed at A and the anode at B, the latent period occurs sooner during a closing contraction than during an opening contraction, as in the former case the stimulus proceeds from A and in the latter from B; and *vice versa*.

2. If the electrodes be placed at the thin edges of a piece of flat muscle, split as in fig. 28, contraction follows, on the passage of a moderate current, in the strip next the cathode on closing, and in that next the anode on opening; of course each fibre has its own cathode and anode, but the density of the current is only sufficient to induce contraction in the neighbourhood of the points where stimulation originates. If the muscle be not split (fig. 29) it bends, for the same reasons, on closure towards the cathode (s) and on opening towards the anode (o).

2. *Chemical stimuli*.—It may be stated in general that whatever effects in a nerve a change of chemical constitution of a certain extent and with a certain degree of rapidity acts upon it as a stimulus. Almost all chemical stimuli cause at the same time the death of the nerve to which they are applied, *i.e.* they destroy its

irritability. But the contrary of this cannot be stated, viz. that all destructive substances act as stimuli; for some of them, as, for instance, ammonia and solutions of metallic salts, produce death so rapidly as to prevent the development of the stimulating effect. Chemical stimuli must, as a rule, be in a more concentrated state for nerves than for muscles, as the substance of the former, especially the sheath, permits but slow diffusion of liquids. The principal chemical stimuli for nerves are the following (Eckhard, Kühne¹): concentrated solutions of the mineral acids, alkalies, alkaline salts, concentrated lactic acid, concentrated glycerin, &c. Deprivation of water (desiccation) also acts as a strong stimulus.

3. *Thermal stimuli*.—A temperature of from 34° to 45°C. acts as a stimulus to the motor nerves of the frog, without producing serious consequences; temperatures up to 40° causing clonic, and temperatures above 40° tetanic, contractions of the connected muscles. Higher temperatures kill the nerve without acting as stimuli (Rosenthal, Afanasieff).

4. *Mechanical stimuli*.—All mechanical impressions which cause alterations of form in any portion of a nerve with a certain degree of rapidity (*e.g.* blows, pressure, ligature, section, &c.) act as stimuli while producing the change. If the form of the nerve has been permanently injured, irritability and conductivity are, as a rule, lost.

5. *Natural stimuli* originating in the end-organs; that is to say, the stimuli induced in the central nervous organs, or in the special nervous terminations of the organs of sense, by the action of light, sound, heat, pressure, &c., which it is the function of the nerves to conduct (consult the Introduction to this Section; and also Chaps. X. and XI.)

Phenomena of the Active Condition.

Concerning the active condition of the nerve itself, very little is as yet known. We know neither the nature of the forces which become free during that condition nor the chemical processes which form their basis. There is absolutely no indication in the case of nerves—such, for instance, as exists in the shortening of muscle—which serves to distinguish an active from an inactive portion; and the only chemical difference which has been insisted upon between nerves which have been at rest and nerves which have been in activity, is (Funke, J. Ranke²), that the latter exhibit an acid reaction; but even this is denied by other observers (Liebreich, Heidenhain³). As little is known about the consumption

¹ Kühne, *Mém. présentés à l'Acad. des Sc. de Paris, dans les Séances du 21 février et du 7 mars 1859.*

² Ranke, *Centralblatt f. d. med. Wissenschaft*, 1868, No. 49.

³ Heidenhain, *Centralblatt*. 1868, No. 53.

of oxygen by active nerves as by inactive nerves. No generation of heat can be shown to take place in active nerves (Helmholtz, Heidenhain). More will be said concerning the electrical appearances and the temporary duration of the activity of nerves when considering their electromotor properties.

*Transmission of the State of Activity along the Nerve-fibres.
(Conduction.)*

The state of activity in a nerve, which, as above mentioned, is accompanied by no external manifestations, leads to change in one of its two end-organs, the peripheral or the central. Under ordinary circumstances, the stimulus, which throws the nerve into the active state, is applied to one of these end-organs, whereupon a certain change, which we are accustomed briefly to call the 'result,' becomes evident in the other. If this 'result' occurs in the central end-organ after stimulation applied to the peripheral, the process is called *centripetal*; and if the contrary, *centrifugal*.

As a rule, only one of these directions is possible in particular nerve-fibres; hence a distinction is made between *centripetal* (or *afferent*) and *centrifugal* (or *efferent*) nerves and nerve-fibres. In addition to this natural method, in which the stimuli are applied to the end-organs, nerves may be artificially stimulated at any point in their course; but in this case also the result takes place in the same way as on natural stimulation, viz. in a central organ in the case of a centripetal fibre, and in a peripheral organ in the case of a centrifugal fibre.

The simplest explanation of this behaviour is that which supposes that on normal stimulation of an end-organ the whole course of the nerve is not thrown into the active condition at once, but that the state of activity is transmitted from one cross section to the next, and so conducted through the whole course of the nerve; that, moreover, any stimulus applied at any point in the course of a nerve-fibre induces the active condition at that point only, whence it is transmitted to the next point, and so on, just as in the case of normal stimulation. This property which nerves have of transmitting the active state from one point to the next until the end-organ is reached is called their *conductivity*. The condition necessary for conduction is that, between the stimulated point and the end-organ in which the result is to be manifest the nerve be quite intact. Lesion at any point in its course through section, pressure (ligature), burning or chemical destruction (treatment with caustics), interrupts conduction. In addition, the other circumstances which diminish irritability act at the same time prejudicially upon conductivity, as, for instance, the anelectrotonic state. The passage of the active condition from one fibre to another never occurs.

Such a passage seems to take place in the case when, on isolated electrical stimulation of one branch of a nerve, contractions follow in a muscle supplied by another branch. This so-called 'paradoxical contraction' will be discussed more at length in treating of the electrical phenomena.

In order to explain the difference between a centripetal and a centrifugal nerve-fibre, it was formerly supposed that every nerve had the power of conducting in one direction only, the former towards the central, the latter towards the peripheral, nervous organs. Such a supposition is, however, unnecessary, as every nerve is connected with one end-organ only which is capable of exhibiting the results of conduction. For example, no nerve exists which is at one end connected with sensory ganglion-cells and at the other with a muscle, in which, therefore, conduction in both directions might be proved. Hence there is no necessity of a specific distinction between centripetal and centrifugal nerves; and we may suppose that all nerves can conduct in both directions, but that only one of the end-organs of each is capable of indicating that conduction. That such a power of conducting in two directions does really exist seems to be indicated by the following circumstances: 1. If a nerve be stimulated at a given point, the electrical changes characteristic of nervous activity appear, not on one, but on both sides of the point of stimulation (du Bois-Reymond). 2. If one terminal twig of a forked motor nerve be stimulated, activity is induced in the other terminal twig, provided the common trunk be intact. The fibres of the former twig must, therefore, have conducted in a centripetal, and not in their usual centrifugal direction (Kühne). 3. No anatomical, chemical, or physiological distinction has hitherto been made out between fibres of the two classes.

The most direct proof, however, of this power of nerves to conduct in opposite directions is an experimental one. If the central portion of a severed sensory nerve be caused to unite with the peripheral portion of a divided motor nerve, an arrangement will have been created for indicating conduction in two directions (Bidder). This experiment has been performed in the case of the peripheral end of the hypoglossal and the central end of the lingual; and the results were such as were anticipated (Philippeaux and Vulpian,¹ Rosenthal). The value of this experiment has lately been questioned by Vulpian himself, because, according to him, the gustatory nerve acquires motor powers on mere section of the hypoglossal nerve, which are to be ascribed to fibres of the chorda tympani which are contained in it; this fact is, however, denied by Eckhardt; further, Vulpian alleges that after union of the gustatory and hypoglossal has occurred, the motor power possessed by the former declines, if the chorda be divided so that its fibres degenerate; the research demands further elucidation.

A physiological distinction between the two classes of nerve-fibres has been sought in the statement that certain poisons affect one kind only; thus it is said, for instance, that the arrow-poison, curare, paralyzes motor nerves alone. It has, however, been shown that the action is one upon peripheral end-organs, and therefore does not affect the properties of the nerves themselves.

¹ Philippeaux et Vulpian, *Mémoires de la Société de Biologie*, 1859, p. 384.

The active condition, therefore, induced first of all at the spot where the stimulus was applied, is transmitted by conduction to the regions on both sides of the spot in the case of a stimulus applied at an intermediate point of the nerve-fibre; or to the region on one side only in the case of a stimulus applied to an end-organ. By this means every portion of the nerve passes successively into the state of activity. It has been observed (Pflüger) that the effect of stimulation, as manifested in an end-organ (e.g. the contraction of a muscle on irritation of a motor nerve) is more marked the farther removed is the point of stimulation from the end-organ. This is explained by supposing that the condition of activity does not travel along a nerve with unaltered force, but that it increases like the momentum of a falling mass ('cascade-' or 'avalanche-effect'). It is, however, more probable that this phenomenon depends upon an increased irritability of the more distant portions of the nerve, due to artificial division where such has taken place, or, perhaps, in other cases, to the proximity of the central organ with which it is connected.

Rapidity of Conduction.

The processes of transmission, upon which conduction depends, take up a definite time. Conduction therefore takes place with a certain, and not very great, degree of rapidity. For the motor nerves of the frog, this rapidity is about 26–27 metres per second (Helmholtz¹). For the sensory nerves of man the determinations vary. The following are some of the principal results of experiments:—

94 metres per second	(Kohlrausch ²)
60	„	(Helmholtz)
34	„	(Hirsch ³)
30	„	(Schelske) ⁴
26	„	(de Jaager ⁵)
41.3	„	(von Wittich ⁶)

For the motor nerves of man, the mean rapidity is about 33.9 metres per second (Helmholtz and Baxt⁷), which is, doubtless, the correct rate for sensory nerves also. Rapidity of conduction is modified by various influences, being diminished, for instance, by cold (Helmholtz), and also by either phase of the electrotonic condition (von Bezold⁸). It is, moreover, probable that rapidity of

¹ Helmholtz, 'Messungen über den zeitlichen Verlauf der Reizung in den Nerven,' *Archiv f. Anat. u. Phys.* 1850, p. 276; and 1852, p. 199.

² Kohlrausch, *Zeitschrift f. Rat. Med.* Vol. xxviii. (1866), p. 190.

³ Hirsch, *Moleschott's Untersuchungen*, vol. ix. 1863, p. 183.

⁴ Schelske, *Archiv f. Anat. u. Phys.* 1864, p. 151.

⁵ Donders and de Jaager, *Nederlandsches Archiv*, vol. i. p. 518.

⁶ v. Wittich, 'Ueber die Fortleitungsgeschwindigkeit im menschlichen Nerven,' *Zeitschrift f. Rat. Medizin*, vol. xxxi. (3rd ser.) p. 87.

⁷ Helmholtz u. Baxt, *Monatsbericht d. Berl. Acad.* 1870, p. 184.

⁸ V. Bezold, *Ueber die elektrische Erregung der Nerven und Muskeln*. 1861, pp. 109–155.

conduction is not uniform, but diminishes as the distance from the place of origin of the stimulation increases (H. Munke, Helmholtz and Baxt).

For the determination of the rapidity of conduction in the motor nerves of the frog the same method is made use of as in the discovery of the time taken up in muscular contraction (p. 272). That is to say, the same nerve is successively stimulated at two different points in its course; on stimulation of a point nearer the muscle the period of latent contraction is of shorter duration than on stimulation of a point more distant, in consequence of which contraction of the muscle occurs more quickly. The duration of the latent period in each case may be registered either by Pouillet's method or by means of the myographion; and the difference of duration, taken in connection with the measured distance between the two points of stimulation, gives the data for determining the required rapidity of conduction in the nerve (Helmholtz).

In the case of man physiologists were formerly limited, in the determination of the rapidity of conduction, to sensory nerves. The general method of procedure is as follows: The person experimented upon gave, on perceiving a certain sensation, a preconcerted signal. The time intervening between this signal and another connected with the stimulus which had given rise to the sensation, was measured by means of one of the numerous instruments devised for such a purpose. Sometimes Pouillet's method was made use of. Hipp's chronoscope (for an account of which see the Text Books of Physics) was another instrument used; as was also Krille's registering apparatus, in which marks were made upon a rotating cylinder, while a pendulum was so arranged as to record seconds on the cylinder at the same time. In Hankel's registering apparatus, which was also used for this purpose, the marks coincident with stimulation and sensation were made by the pressure of a pencil upon a surface of paraffin fixed at the circumference of a quickly revolving wheel, while the rate of rotation of the wheel was checked by means of Krille's instrument. Another instrument was König's phonautograph, on the same principle as Krille's, except that a vibrating tuning-fork recorded time instead of a pendulum; the object of this improvement being to register much smaller intervals than is possible with a pendulum, a most important point when the rate of rotation varies. The time, so measured, is divisible into three portions: *a* the time taken up by the passage of the sensation to the brain; *b* the time occupied in the perception of sensation and the origination of motor impulse; *c* the time which elapses from that origination to the occurrence of the pre-arranged signal, that is to say, $T = a + b + c$. If now the experiment be twice made, once with a stimulus applied at a point near the brain, and once at a point more remote (say at the neck and at the foot respectively), the difference between the two times *T* and *T'*, considered in relation with the difference in length of the nerve traversed, would give the desired rapidity of conduction: supposing always that the difference between *T* and *T'* consists of that between *a* and *a'* only, and that *b* and *c* remain the same in both experiments. The latter supposition, however, with regard to *b*, cannot always be relied upon as holding; for it has been found that the kind of sensation, a previous knowledge or ignorance of it, the expectation of it at a given time, the character of the pre-arranged signals, &c., have the greatest influence upon the time (Donders and de Jaager). The great difference observable in the determinations of various observers may, therefore, depend either upon the inconstancy of the factor *b* or upon real individual differences of conductive power.

The rate of conduction of motor nerves of man is determined by tracing upon a myograph the curve of contraction of the muscles of the thumb by means of their increase in thickness. Two tracings must be taken, one when the stimulus has been applied to the nerve at a point on the arm near to the hand, and the other when it has been applied at a point more remote from the hand, from which the determination is easily made (Helmholtz). It may be mentioned, by the way, that weak stimuli were found during these experiments to be conducted more slowly than strong ones.

Electrical Phenomena of Nerves.

1. *Action of Galvanic Currents upon Nerves.*

The resistance of nerves to electrical conduction is about five times as great in a direction across, as in the direction of, the fibres; by the process of death this difference is diminished by about one-half. The cause of this condition is altogether or in part an internal polarization, which appears at the border between the sheath and contents of the nerve-tube. This polarization develops instantly on closing, and vanishes as suddenly on opening, the current in the course of which the nerve is placed. Similar phenomena are noticed in the case of muscles, in which the resistance in a transverse direction is seven times as great as that in a longitudinal direction (Hermann¹).

The resistance offered by nerves to conduction across them ('Querwiderstand') is not affected by stimulation (Hermann); the apparent diminution of the resistance in a longitudinal direction (Grünhagen) depends upon the changes in excitability which occur in the part of the nerve through which a current is passing. These will be treated of in the sequel.

During electrotonus a current having the same direction as the polarizing current is everywhere demonstrable in the extra-polar region, and adds itself algebraically to the current of repose, where such is present. This electrotonic current is strongest in the region of the electrodes. It appears immediately on closing, and is constantly diminishing on the side of the cathode (du Bois-Reymond). No current in the same direction as the polarizing current is known to exist in the intra-polar region, in addition to the polarizing current itself (Hermann).

The sudden appearance of the electrotonic current in the extra-polar regions may act as a stimulus upon neighbouring nerves, thus causing 'secondary contraction or secondary tetanus' (p. 290); of such a nature is the 'paradoxical contraction,' already mentioned, which follows in a muscle connected with one branch of a nerve after the electrical stimulation of another branch of the same nerve. It is explained by supposing that the contiguity of the fibres of the two branches gives opportunity for the sudden appearance of the electrotonic current in the one to act as a stimulus upon the other (du Bois-Reymond).

After breaking the polarizing current certain 'after-currents' remain (Fick) for a short time. In the intra-polar and anelectrotonized extra-polar regions they have the opposite direction to the polarizing current; but in the catelectrotonized extra-polar region the 'after-current' has the same direction as the polarizing current (Hermann).

The electromotive force of electrotonic currents is very great. Some electrotonic currents have been observed to possess electromotive force equal to half that of a Daniell's element (du Bois-Reymond).

¹ Hermann, *Pflüger's Archiv*, vol. xii, p. 151.

2. *Essential Electrical Properties of Nerves.*

In a portion of nerve bounded by two transverse sections, the existence of currents is demonstrable which obey the same laws as those of muscle (du Bois-Reymond,¹ consult p. 285 *et seq.*)

No currents have with certainty been detected at any natural cross-section of a nerve.

The electromotive force of the current passing from longitudinal to transverse sections of a nerve is, as a rule, equal to about $\cdot 02$ of a Daniell's element (du Bois-Reymond). As far as yet investigated, temperature appears to affect it in the same manner as it does the muscular current.

On stimulation of a nerve the electromotive force of the essential nerve-current is diminished (du Bois-Reymond). This 'negative variation,' which, if the stimulus is strong enough, may proceed to the reversal of the nerve-current, develops more quickly than it disappears, and occupies altogether about $\cdot 0007$ of a second (Bernstein²). In polarized nerves the extra-polar electrotonic currents also exhibit a 'negative variation' on stimulation (Bernstein); in the intra-polar region stimulation induces the appearance of an accessory current in the same direction as the polarizing current (Hermann).

Stimulation applied to a nerve-trunk is evidenced by the negative variation of its proper current, just as a stimulation of intramuscular nerve-terminations is evidenced by muscular contraction. The same use may, therefore, be made of negative variation, as of the contraction of muscle, for the discovery of the laws of stimulation of nerves. Both, for example, are diminished if the region of stimulation be already anelectrotonized, and increased if it be catelectronized (Bernstein); and the interval of time between stimulation and the occurrence of the negative variation may be used, in the same way as the interval between stimulation and contraction, in determining the rapidity of conduction (Bernstein). Since the difficulty is great of arranging nerves so as that both ends shall be connected with muscles, whilst it is easy to have a nerve with two artificial transverse sections, negative variation affords the simplest means of proof of the power of nerves to conduct in opposite directions (du Bois-Reymond).

It is, moreover, necessary, just as in the case of muscle, to apply to nerves a considerable number of rapidly succeeding stimuli in order to indicate the negative variation of their currents by the needle of a galvanometer. It is not possible, as a rule, to get evidence of negative variation by means of the physiological rheoscope, as 'secondary contraction and secondary tetanus' proceeding from nerves are not caused by the negative variation of the proper currents of

¹ [Throughout the sections devoted to the discussion of the electromotive properties of muscle and nerve, reference is continually being made to the researches of du Bois-Reymond. These will be found in the two great collections of the scientific writings of this distinguished physiologist. The first of these collections, entitled *Untersuchungen über Thierische Elektrizität*, comprised three volumes, of which the first appeared in 1848, the first part of the second in 1849, and the second part of the latter in 1860. In these volumes the author, besides giving a critical history of all former researches on animal electricity, collected all the results of his own investigations prior to the dates of their publication. The second series of collected writings appeared under the title of *Gesammelte Abhandlungen zur allgemeinen Muskel- und Nervenphysik* (Leipzig, Verlag von Veit u. Comp.), the first volume (398 pages) appearing in 1875, and the second (753 pages) in 1877.]

² Bernstein, 'Untersuchungen über d. Erregungsvorgang im Nerven- und Muskel-systeme.' 1871.

the latter, but by the currents due to electrotonus. For example, 'secondary contraction' does not follow at all when the stimulus applied to the nerve is not electrical; and it may be shown by means of the Law of Contraction that, under certain circumstances, 'secondary contraction' depends upon a stimulation of the rheoscopic nerve due to a *positive* variation, such, *e.g.*, as that caused by the appearance or disappearance of electrotonus (du Bois-Reymond). The following experiment serves for determining the length of time which elapses between stimulation and the occurrence of negative variation (Bernstein): A quickly-revolving wheel causes at each revolution, (1) the electrical stimulation of a point, *a*, of the nerve, and immediately afterwards (2) the transitory closure of a circuit which includes a galvanometer and a portion of nerve *b*, arranged as for the demonstration of its natural current. The interval of time between (1) and (2) can be varied at will; and, by gradually increasing it from 0, a point is at last reached at which closure of the galvanometer-circuit exactly coincides with the commencement in the region *b* of the negative variation due to the stimulation of *a*. The time thus determined clearly indicates the period required for the effect of the irritation to travel from *a* to *b*. This period is proportional to the length of nerve between *a* and *b* (whence it immediately follows that the effect of stimulation commences the moment it is applied); and from the data it has been calculated that irritation travels at the rate of 28·718 metres per second.

If the time between (1) and (2) be so arranged that the nerve-current in *b* shows, at the moment of closure of the galvanometer-circuit, not the beginning but some other phase of the negative variation, say the maximum, or the end, it is possible to determine from the time intervening between (1) and (2) the duration and progress in time of the negative variation itself.

There are two theories regarding the currents of nerves as of muscles. According to the 'Pre-existence Theory' (du Bois-Reymond) every nerve-fibre contains regularly arranged electromotive

FIG. 50.

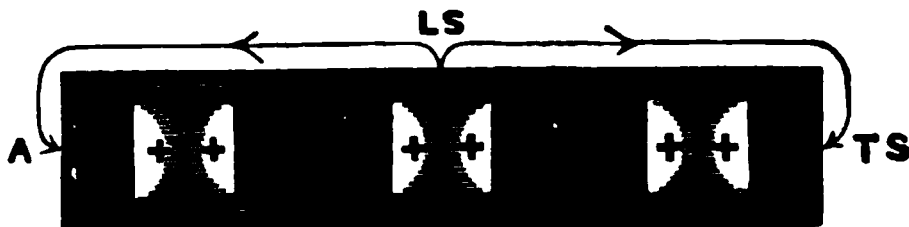


DIAGRAM EXHIBITING THE HYPOTHETICAL ARRANGEMENT OF ELECTROMOTOR MOLECULES IN MUSCLE, AND THE DIRECTION OF THE MUSCULAR CURRENT.

L s is the longitudinal surface, T s is the transverse surface, of the muscle.

molecules, which present their positive elements to a longitudinal, and their negative elements to a transverse, section, and whose activity diminishes on stimulation. Electrotonic currents are explained, according to this hypothesis, by attributing to the polarizing current a directive action upon the movable molecules, which are supposed to be so turned as to have the same direction as the polarizer. In order that this should be possible, each molecule must be supposed to be divided into two bipolar halves, incapable of mechanical or chemical separation, each of which can, however, rotate about an axis of its own. By this means an arrangement of the halved molecules end to end is possible, which is most complete in the neighbourhood of the polarizing electrodes, and which explains the electrotonic current.

In opposition to this explanation of electrotonic currents may be cited the condition of the intrapolar region. According to the above theory this region should exhibit an extremely powerful accessory current in the same direction as the polarizer, whereas there is no trace of such a current.

The 'Difference Theory' (Hermann) explains the natural current of nerves, like that of muscles, as the effect of contact; the contents of nerve-tubes which are dying or in activity are negative to the contents of nerve-tubes which are living and at rest. The cause of the electrotonic phenomena is the polarization at the boundary between nerve-sheath and contents to which reference has already been made.

If a current passes from one conductor to another, and if at the boundary between them polarization, and, in consequence, a change of resistance occur, both current and state of polarization spread out over the region about the points of entrance and exit. In consequence of this any pair of electrodes situated in an extra-polar region receives a branch of the current having the same direction as the polarizing current. In the intra-polar region the branches of the original current would be found, if it were possible to demonstrate them, to have a direction opposite to that of the polarizer. This circumstance, which was first shown to occur in the case of moist, covered wires (Matteucci), is taken to explain electrotonus in nerves, as in the latter the necessary conditions are present (Hermann). The polarization-currents continue a short time after the polarizer is broken; but in the anelectrotonic area the more powerful effect of the opening or breaking shock at the anode produces the appearance of reversal of the after-current, which flows in an opposite direction to the polarizer (see above).

If, as was assumed on page 341, conduction in a nerve is nothing but the transmission of the condition of activity from one portion to another, then both the above theories of the nerve-current must require that, while a nerve is conducting, the point of it at which the active condition for the moment obtains must be negative towards every other point in the long axis of the nerve. No direct indication of such a condition has as yet been obtained.

The alterations of electrotonic currents effected by stimulation may be explained by assuming that the effect of stimulation in its course through the polarized nerve varies in intensity, increasing when it reaches a point which is more positive (*i.e.* which is more strongly positively, or more weakly negatively, polarized), and diminishing when it reaches a point which is more negative. In this way are explained: 1. The positive increase of current in the intra-polar region; for the effect of stimulation is more powerful as it reaches the anode than as it reaches the cathode, and in consequence the former becomes through irritation more strongly negative than the latter. 2. Similarly the diminution in extra-polar electrotonus. 3. The negative variation of the proper nerve-current; for the latter causes negative polarization in the neighbourhood of the transverse section, in consequence of which the effect of stimulation is less powerful by the time it has reached the transverse section, and every longitudinal section therefore becomes on irritation more strongly negative than a transverse section. It follows on the contrary from the same supposition that any irrita-

tion arising in a positively polarized (anelectrotonic) portion of nerve must diminish in its course through the nerve, while any irritation arising in a negatively polarized (catelectrotonic) portion must increase. Hence we can see the cause of the apparent diminution of irritability which occurs during anelectrotonus, and of the apparent increase during catelectrotonus (and in the neighbourhood of the transverse section). The phenomena described on page 339 may also in this way be explained (Hermann).

Theories concerning the Nature of Nervous Activity.

Most thinkers on the subject assume the existence in nerves of movable or alterable particles, so connected together that the movement or alteration of any one leads to the movement or alteration of those in its immediate neighbourhood. Many identify these particles with those which are assumed for the purpose of explaining the electromotive properties (p. 348) of nerves. It is further supposed that the movement or alteration of which the particles are capable, takes place in opposition to resistances or inhibitions whose power is inversely proportional to the irritability of the nerve. These inhibitions or resistances are diminished in catelectrotonus and increased in anelectrotonus.

The motion or alteration of one of the nerve-particles would, therefore, act like a stimulus on the next, whereby it seems to be implied that conductivity proceeds *pari passu* with irritability. The latter is not apparently always the case. Thus, in the catelectrotonic condition, irritability is increased while the rapidity of conduction diminishes; in the spinal cord there are said to exist conducting fibres which are incapable of direct stimulation (Chap. XI.); and nerves poisoned by conine, curare, or carbonic acid, as well as occasionally the nerves of paralyzed parts, are said to be still able to conduct irritations from the nervous centres, but are incapable of direct stimulation (Schiff, Erb, Grön-hagen).

There are various views as to the nature of the process of stimulation. Some are inclined to imagine a real movement (rotation, deviation, &c.); others a chemical change, a decomposition analogous to that which takes place in muscle, and which sets free a similar process in neighbouring particles somewhat as fire travels along a train of gunpowder. This decomposition would occur slowly even during repose, and would be accelerated by death and the influences increasing irritability. Stimuli (influences suddenly working) would cause great acceleration, and the impulse to decomposition would be imparted to the neighbouring particles the more quickly according as the rapidity of the process was greater. Death spreads slowly, and irritation quickly, through nerves; the latter the more quickly according as it is stronger.

Polarization which occurs at the border between the sheath and contents of a nerve-tube, and upon which electrotonus depends (p. 346), possibly plays an important rôle in the transmission of irritation. As, for instance, a stimulated portion of the interior of a nerve is electrically negative to the surrounding portions which have not been stimulated, small currents arise which tend to equalise through the sheathing substance. They have, however, the effect of producing anelectrotonus, and therefore of inhibiting excitation at the point of stimulation, and of causing catelectrotonus, with the accompanying excitation, in the surrounding non-stimulated portions.

The Function and Classification of Nerve-Fibres.

Although it is highly probable that all nerve-fibres are perfectly alike (p. 343), some classification of them is expedient. The usual division is founded upon the accidental function of the fibres as indicated by the arrangement of their end-organs. The function of a nerve thus determined is called its 'specific energy.' All nerve-fibres, or, more exactly, all nerve-fibres with their accompanying end-organs, may, therefore, be divided into:

A. *Centrifugally conducting* or '*Efferent*' fibres (p. 342): 1. Motor fibres, at the peripheral end of which is a muscular fibre or another of the contractile elements mentioned in the preceding Chapter; 2. Secreting fibres, at the peripheral extremity of which stands a glandular element, and whose specific energy consists in stimulating increased secretion in glands, without the aid of the vaso-motor apparatus, on reflex or central excitation; 3. Trophic fibres, *i.e.* such as regulate the processes of nutrition (oxidation) in the various parenchymata, and therefore have the same relation to the parenchymatous juices as secreting fibres to free secretions. Their existence, although not improbable, has never yet been demonstrated. Almost all the phenomena which have hitherto been cited to prove their existence may be referred to the action of motor (and especially vaso-motor), secreting and even sensory fibres, as will be stated in describing the trigeminal nerve. The only undoubted case of nervous influence on nutrition is that of the influence on the nutrition of nerves themselves. It has been previously stated that divided nerves undergo fatty degeneration in their peripheral portions.

The secreting nerves, and the trophic nerves if they exist, also influence the formation of heat, and might, therefore, be described as thermic, just as muscular nerves are described as motor. The influence of nerves upon local temperatures appears, however, to be connected with the distribution of blood (vaso-motor nerves).

B. *Centripetally conducting* or '*Afferent*' fibres:—1. Sensory fibres, the central end-organ of which is an organ of the mind, and the result of irritation of which is a mental operation, *viz.* sensation; their peripheral end-organs are organs of sense (Chap. X.); 2. Reflex, or excito-motor, fibres, in the central end-organ of which the irritation which has traversed the fibre to that point is transferred to another fibre, and finally to a centrifugal system.

The central organs connected with the sensory fibres have to do with various kinds of sensations, some with sensation of sight, others with sensations of hearing, &c. The same sensory fibre

always calls into action the same portion of the mental apparatus, and always therefore produces the same sort of sensation, in whatever way it is stimulated. Hence, the 'specific energy' of the optic fibres is the transmission of visual impressions, that of the acoustic fibres the transmission of auditory impressions, &c. Further, it is necessary to ascribe to the irritation of different fibres the different qualities of any given sensation, *e.g.* the sensation of red and of blue light, or of high and of low notes, and hence, to suppose that certain fibres have, as their 'specific energy,' to aid in the perception of the red rays, while that of others is to assist in the perception of the blue. For, if it were not so, we should be compelled to assume that one and the same nerve-fibre was capable of states of irritation which were qualitatively different—an assumption hitherto entirely unsupported by facts. There must, therefore, be at least as many sensory fibres as simple qualities of sensation, and the student may be reminded that the innumerable varieties and shades of sensation which are actually experienced arise from the mingling in various ways of a relatively small number of simpler qualities (Chap. X.) Although this logical consequence of the principle of specific energy (Young, Helmholtz) is a physiological postulate, it is as yet only applicable to a few of the organs of sense.

This principle is apparently at variance with our experience that the nerves of taste occasion different sensations, according as they are stimulated by ascending or descending currents. The experiments in question, however, admit of another explanation (Chap. X.)

The peripheral end-organ of every sensory nerve (organ of sense), and such organ alone—is capable of excitation not only by the stimuli common to all nerves, but also by one peculiar to itself, which constitutes its usual means of excitation. Thus the end-organs of the optic fibres in the retina are excited by waves of light; those of the acoustic fibres by waves of sound; those of the olfactory fibres under the influence of odorous bodies, &c.

As the mind has no means of recognising the origin of any given stimulation, it assumes that all sensations come from their usual source. For example: (1) It refers the origin of every sensation which reaches it through a sensory fibre to the end-organ of that fibre, even though stimulation has not been applied in the usual manner but to the trunk of the nerve. Thus, persons who have had a limb amputated feel sensations caused by any irritation of the stump of the nerve as if they arose in the amputated limb (eccentric reference of sensations). (2) In the case of special sensations it assumes the stimulus to have been that which usually causes the same sensation (light, sound, &c.), notwithstanding that any of the common nervous stimuli (mechanical, electrical, thermal or chemical) may have originated it. Thus it considers every visual sensation as occasioned by waves of light which have im-

pinged upon the retina, even though mechanical disturbance of the retina, pressure on the optic nerve, &c. may have been the cause. The conclusions arrived at by the mind concerning the origin of stimulation go in many cases still further, as, for example, when the stimulus proper to a given organ of sense always takes the same path in order to reach it. Thus, it supposes every wave of light impinging upon the retina, or every wave of sound acting upon the acoustic nerve, to have previously traversed the transparent media of the eye, or the conductors of sound of the ear, as the case may be. Hence, it refers the causes of all sensations of light or sound to without. In the case of visual sensations the mind even forms a judgment as to the *position* of the illuminating body, or at least as to its direction. In the act of seeing, every illuminated point of the retina may be connected with the point whence the rays of light proceed by means of the axial ray of the particular pencil illuminating that point (Chap. X.), and the cause of the visual sensation is referred to the external medium in the direction of this ray, even though that cause be subjective.

C. *Intercentral fibres*; that is to say, such as unite two central organs (ganglion-cells). Their number is enormous, and their function, which is as yet only hypothetical, will be discussed in Chapter XI. The following are included under this head: the majority of the fibres of the brain and spinal cord; the chief portion of the sympathetic nerves; the so-called inhibitory nerves; &c.

B. SPECIAL PHYSIOLOGY OF NERVES.

The various nervous fibres, motor, sensory, &c., are so arranged as a rule that all those destined for the same region of the body, of whatever sort they are, run together for a certain distance in one 'mixed' nerve-trunk, which gives off branches composed of one kind of fibres only ('sensory nerves,' 'motor nerves') when the locality about to be supplied by those branches is almost reached. In the case of cranial nerves, the whole course of which is short, this union is rarely if ever effected. Cranial nerves are, therefore, from their origin for the most part either purely motor or purely sensory.

The object of the special physiology of nerves is to determine for each nerve-fibre its specific energy, which is called for the sake of brevity its 'function.' This would be self-apparent in the case of any fibre, if its two-end organs were anatomically known and their functions understood. Here the two sciences of anatomy and physiology mutually supplement one another.

In order to determine the special function of a nerve the following methods are adopted:

1. A nerve is divided at any point. Stimulation applied to the nerve on

that side of the point of section remote from the organ in which the results of excitation would follow normally no longer produces the customary results. Thus, if it is a muscular nerve which has been divided, the muscles connected with it remain inactive although the will, or a reflex or automatic stimulus, or any other excitant applied to the nerve above the place of section, are still operative,—the muscle is ‘paralysed;’ while, if the nerve is centripetal, stimulation of the sense-organ, or excitation of the peripheral portion of the nerve, no longer induces sensations, and blindness, deafness, insensibility, &c. follow.

2. The two ends of a divided nerve are stimulated (usually tetanically), and observations are made as to which end is affected, and what the nature of the result.

I. Spinal Nerves.

Concerning the central connections and origin of the spinal nerves, see Chapter XI.

The nerves which spring from the spinal cord are all, through the greater part of their course, mixed; yet they are not mixed at their origin, for each spinal nerve springs from two roots; an anterior root which contains the efferent, and a posterior root which contains the afferent, fibres (Charles Bell (1)); the former is called the *motor*, the latter the *sensory*, root; the sensory root possesses a *ganglion*.

If all the anterior roots of one side of the body be divided, the muscles of the corresponding half of the body are completely paralyzed; if the posterior roots be divided instead, then the corresponding half of the body becomes insensitive. If, in a frog, the posterior roots be divided on one side of the cord (*e.g.* on the right) and the anterior roots on the opposite (left) side, on inflicting some injury to the right leg the creature remains motionless, as it does not feel pain; if the left leg be, however, injured, defensive movements are made with the right leg, whilst the left leg remains motionless, for the creature is conscious of pain in the left leg, but can only move the right leg. When it jumps it drags even its right leg behind it, because it does not feel that leg.

The fact that even the anterior roots are sensitive (Longet) is no contradiction of Bell’s law: for when these are cut across it is only the peripheral, and not the central, end which is sensitive (Magendie); the mixed sensory fibres come, therefore, from the periphery, and all sensibility ceases on division of the posterior roots (*‘sensibilité récurrente’*). Even after division of the anterior roots their central cord contains a number of degenerated, and their peripheral ends a number of undegenerated, fibres (Schiff, Vulpian). The bending in of sensory fibres into motor tracts occurs near the peripheral ends of the nerves; sensory fibres sometimes bend into other sensory paths, so that the peripheral end of a divided sensory nerve is generally sensitive (Arloing and Tripier). The nervous distribution to the head affords instances of *‘sensibilité récurrente’* which depends upon sensory fibres of the fifth.

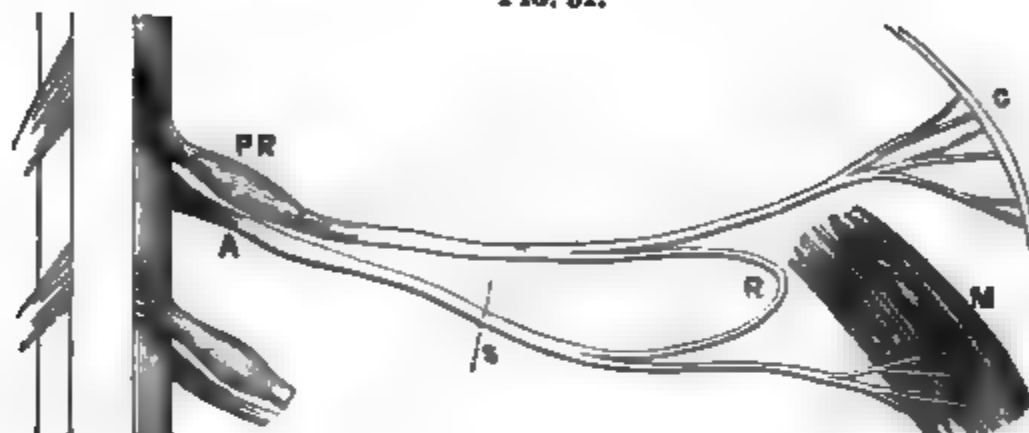
[In the annexed diagram the mechanism of recurrent sensibility is illustrated.]

The two roots of a spinal nerve are shown schematically, their fibres being for simplicity kept from uniting into one trunk. P R is the posterior root, and A is the anterior root. The posterior root is seen to terminate in s, which indi-

ates the skin or other sensory structure. The fibres from the anterior root, on the other hand, terminate in *M*, which represents muscular fibres. *B* represents a loop of sensory fibres passing from the posterior root and bending in to join *A* the anterior root, and furnishing it with 'sensibilité récurrente.'

Were a section to be made through the fibres of *A* at *s*, and the distal end stimulated, pain would be felt by the animal in consequence of the sensory fibres which had joined the motor fibres through the loop *B* being stimulated; all effect of the stimulation would, however, cease on the division of the posterior root *P R*.

FIG. 81.



When the posterior roots of the spinal nerves are cut across, the excitability of the anterior roots suddenly undergoes diminution (Ludwig and Oyon, contradicted by Grünhagen and G. Heidenhain). The former must, therefore, by a reflex process continually increase the excitability of the latter, or (which is more intelligible) continually excite the latter, so that, on stimulating the anterior roots, the stimulation adds itself to the already present stimulation.

The *centrifugal* or *efferent* fibres of the spinal contained in the anterior roots are: 1, *motor* for all the striated muscles of the trunk and the extremities and (probably through the medium of the sympathetic) for certain smooth muscles of the viscera, e.g. the *detrusor urinæ*; 2, *vaso-constrictor* and *vaso-dilator* fibres for the arteries of the body: these, however, pass in part into the sympathetic and afterwards pass into other spinal nerves; 3, possibly also *secretory* and *trophic* fibres. The *centripetal* or *afferent* fibres are the *sensory* fibres for the whole of the surface of the body; with the exception of the face and anterior part of the head.

The distribution of the various motor and sensory nerves which spring from the thirty-one pairs of spinal roots, belongs to the province of descriptive anatomy.

[When the anterior root or a spinal nerve is cut across, the nerve-fibres contained in the distal end undergo a fatty degeneration, whilst those which retain their connection with the grey matter of the cord remain unaltered. When the posterior root of a spinal nerve is divided on the distal side of the ganglion, the fibres which have been separated from the ganglion degenerate, whilst those which are connected with it do not. When the posterior root of a spinal nerve is divided on the proximal side of the ganglion, the fibres attached to the spinal cord degenerate, whilst those which retain their connection with the ganglion do not.]

These facts would appear to indicate that the nutrition of fibres of the anterior root is influenced by their central connections in the spinal cord, whilst

the nutrition of fibres of the posterior roots is under the control of the ganglion or the posterior roots. Both sets of fibres degenerate, however, when cut off from the nerve-centres which respectively influence their nutrition. A knowledge of this degeneration of nerve-fibres cut off from their centres has supplied a method whereby to trace the distribution of nerve-fibres, called, after its discoverer, the 'Wallerian Method.']

II. Cranial Nerves.

For the origins of the Cranial Nerves refer to Chapter XI.

First Pair (Olfactory Nerve).

The fibres of this nerve have the function of conducting every irritation, at whatever point of their course it originates, to that part of the brain concerned in the perception of smell, thereby giving rise to the sensation of smell. In the physiological condition the excitation always affects the peripheral end-organs of the nerve situated in the olfactory membrane, and is occasioned by certain specific stimuli, 'odorous bodies.' Section of the olfactory bulbs, which is practicable in the case of young animals, destroys the sense of smell (Biffi). [Such section does not, however, destroy the common sensibility of the nasal cavities, which depends upon the branches of the fifth nerve distributed to the nasal cavities; powerful irritants such as ammonia are therefore able to excite sensations even after section of the olfactory bulbs. The functions of the olfactory nerve will be found fully discussed under the head of Olfactory Organ.]

The production of sensations of smell on stimulation of the olfactory nerves, by means of ordinary nerve-stimuli, has not yet been directly demonstrated.

Second Pair (Optic Nerve).

All stimulations of this nerve cause stimulation of that portion of the brain concerned in the perception of light, and, in consequence, produce sensations of light. Normally stimulation originates in the peripheral terminations of its fibres in the retina. It possesses, in addition, the power of inducing by reflex action the contraction of the sphincter of the iris, through fibres of the third nerve proceeding to that muscle. The Optic Chiasma is discussed in Chapter X.

Third Pair of Nerves (Motorius oculi).

This nerve is the motor nerve for most of the muscles of the orbit, viz. for the rectus sup., rectus inf., rectus int., obliquus inf., and levator palpebræ superioris; for the circular muscle

of the iris and for the ciliary muscle. Its excitation in part is due to the voluntary action of the brain, but those of its fibres which are supplied to the iris may be excited in a reflex manner through the optic nerve (Chapter X.) It has been surmised that the third nerve contains some sensory fibres; a surmise based upon the observation of a 'sensibilité récurrente' depending upon the fifth nerve.

In fig. 32, p. 358, the third nerve is shown diagrammatically, together with other nerves of the orbit. It is seen dividing into an upper division (4) which is distributed to the rectus superior and the levator palpebræ superioris, and a lower division (5) which supplies the rectus inferior, rectus internus, and the inferior oblique; the nerve to the latter furnishes one of the roots (the *short root*) of the ophthalmic ganglion. It is through this root that the efferent fibres enter which subsequently are distributed in the *short ciliary nerves* to the sphincter iridis and the ciliary muscle.

Section and paralysis of the third nerve causes: 1. Drooping of the upper eyelid, 'ptosis' [by paralyzing the levator palpebræ superioris; under these circumstances a still firmer closure of the eye can be brought about by the contraction of the orbicularis palpebrarum]. 2. Rotation outwards of the eyeball, since the muscles supplied by it can no longer balance those supplied by the fourth (trochlear) and sixth (abducens) nerves. [In consequence of this paralysis the rotatory movements of the eyeball about its axis are impaired. When the head is moved from one side to another the eye is unable, as in the physiological condition, to move in the opposite direction, and therefore follows the movements of the head. Amongst other results of the muscular paralysis dependent upon lesion of the third nerve are, *a*, a form of diplopia or double vision, and, *b*, some degree of protrusion of the eyeball.] 3. Dilatation and insensibility to light of the pupil. 4. A persistent state of accommodation for long distances [i.e. an inability to accommodate for near objects].

Fourth Pair (N. trochlearis, N. patheticus).

This is the motor nerve for the superior oblique. The existence of sensory fibres in this nerve has been maintained by some.

[When the fourth nerve on one side is paralysed the eye is moved slightly upwards and outwards; the rotation of the eyeball is impaired; when the patient looks down (but only then), there is diplopia; the double images seen under these circumstances are not crossed, and the image seen by the sound eye appears to be more distant and higher than that seen by the injured eye.¹]

Fifth Pair (N. trigeminus).

This is a mixed nerve arising after the fashion of a spinal nerve by two roots, a sensory (large), and a motor (small). The sensory root, like the sensory root of a spinal nerve, possesses a ganglion—the Gasserian or semilunar ganglion.

[From the latter three branches or divisions are given off, named respectively the first or ophthalmic division of the fifth, the second division of the fifth or superior maxillary nerve, and the

¹ Longet, *Traité de Physiologie*. Tome iii. p. 560.

the nutrition of fibres of the posterior roots is under the control of the ganglia or the posterior roots. Both sets of fibres degenerate, however, when cut off from the nerve-centres which respectively influence their nutrition. A knowledge of this degeneration of nerve-fibres cut off from their centres has supplied a method whereby to trace the distribution of nerve-fibres, called, after its discoverer, the 'Wallerian Method.']

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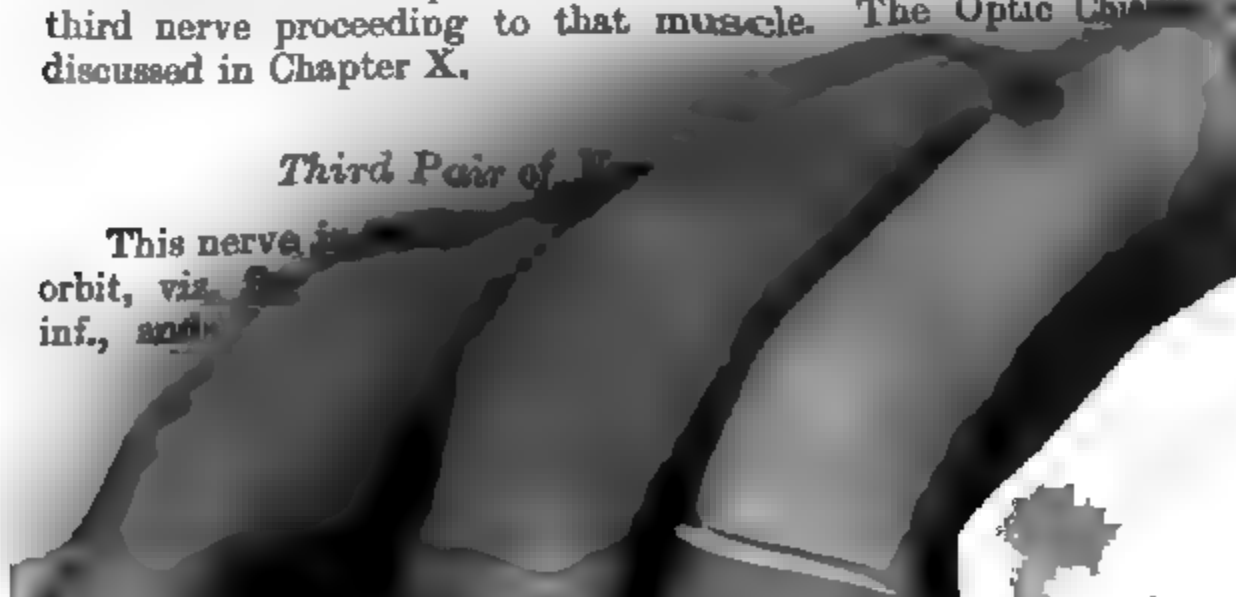
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Third Pair of Nerves.

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inf., and



the iris and for the ciliary muscle. Its excitation in part is due to the voluntary action of the brain, but those of its fibres which are supplied to the iris may be excited in a reflex manner through the optic nerve (Chapter X.) It has been surmised that the third nerve contains some sensory fibres: a surmise based upon the observation of a 'sensibilité récurrente' depending upon the third nerve.

In fig. 32, p. 352, the third nerve is shown diagrammatically, together with other nerves of the orbit. It is seen dividing into an upper division (4) which is distributed to the rectus superior and the levator palpebræ superioris, and a lower division (5) which supplies the rectus inferior, rectus internus, and the inferior oblique; the nerve to the latter furnishes one of the roots (the short root) of the ophthalmic ganglion. It is through this root that the efferent fibres enter which subsequently are distributed in the short ciliary nerves to the sphincter iridis and the ciliary muscle.

Section and paralysis of the third nerve causes: 1. Drooping of the upper eyelid, 'ptosis' [by paralyzing the levator palpebræ superioris: under these circumstances a still firmer closure of the eye can be brought about by the contraction of the orbicularis palpebrarum]. 2. Rotation outwards of the eyeball, as the muscles supplied by it can no longer balance those supplied by the fourth (trochlear) and sixth (abducens) nerves. [In consequence of this paralysis the rotatory movements of the eyeball about its axis are impaired. When the head is moved from one side to another the eye is unable, as in the physiological condition, to move in the opposite direction, and therefore follows the movements of the head. Amongst other results of the muscular paralysis dependent upon lesion of the third nerve are, a, a form of diplopia or double vision, b, some degree of protrusion of the eyeball.] 3. Dilatation and insensibility to light of the pupil. 4. A persistent state of accommodation for long distances [i.e. an inability to accommodate for near objects].

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When the fourth nerve on one side is paralyzed the eye is moved slightly upwards and outwards; the rotation of the eyeball is impaired; when the eye looks down (but only then), there is diplopia; the double images seen in these circumstances are not crossed, and the image seen by the sound eye is to be more distant and higher than that seen by the injured eye.*

Fifth Pair (N. trigeminus).

It is a mixed nerve arising after the fashion of a spinal nerve from two roots, a sensory (large), and a motor (small). The sensory root, like the sensory root of a spinal nerve, possesses a Gasserian or semilunar ganglion.

The latter three branches or divisions are given off, named the first or ophthalmic division of the fifth, the second or maxillary division of the fifth or superior maxillary nerve, and the third or mandibular division of the fifth or inferior maxillary nerve.

* *Longet, Traité de Physiologie. Tome iii. p. 560.*

third division of the fifth or inferior maxillary nerve, which is joined by the small or motor root of the nerve.

The relations of the two roots of the fifth are seen in the diagram of the third division of the fifth nerve (p. 361). In fig. 82, a diagrammatic view of the ophthalmic or first division of the fifth nerve is given. The Gasserian ganglion is seen giving off its three divisions *a*, *b*, and *c*, of which *a* is the ophthalmic division. This division splits up into three branches: its frontal branch (1), the largest, which divides into two branches, supra-trochlear and

FIG. 82.

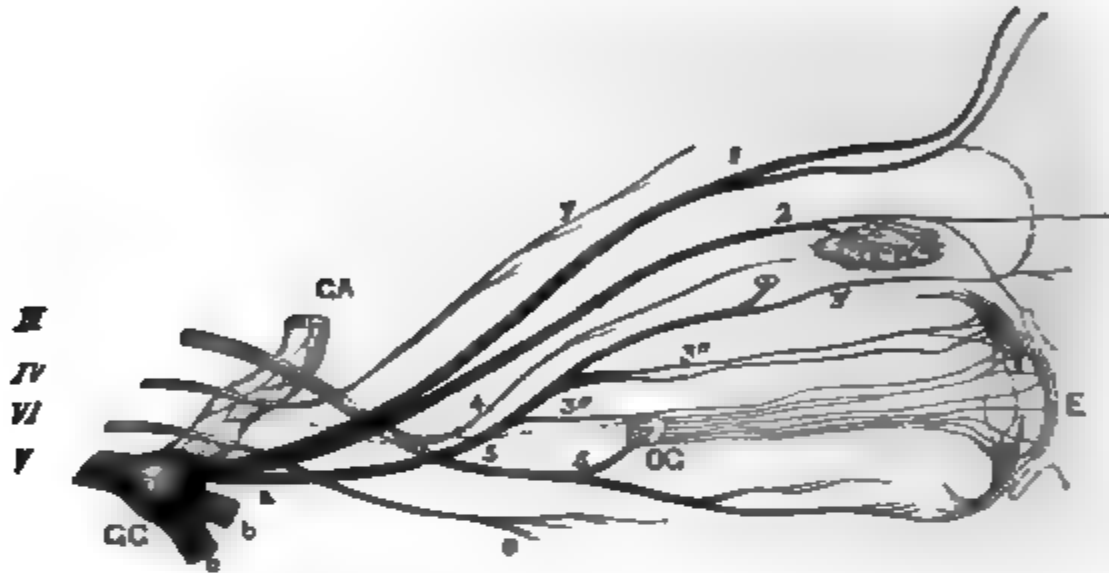


DIAGRAM OF THE FIRST OR OPHTHALMIC DIVISION OF THE FIFTH, SHOWING ALSO THE THIRD, FOURTH, AND SIXTH CRANIAL NERVE.

- V. Sensory root of fifth nerve.
- G.C. Gasserian ganglion on larger root of the fifth nerve.
- a ophthalmic division of the fifth nerve.
 - 1. frontal nerve. 2. lacrimal nerve. 3. nasal nerve.
- L.G. lacrimal gland.
 - 1' infra-trochlear branch of nasal nerve.
 - 1'' long ciliary branches of nasal nerve.
 - 1''' branch of nasal nerve to ophthalmic ganglion.
- O.G. ophthalmic ganglion.
 - b second division of fifth cut across. c third division of fifth cut across.
- III. third nerve (motorius oculi).
 - 4. upper division of third nerve.
 - 5. lower division of third nerve, near point where it gives the short root to the ophthalmic ganglion.
- IV. fourth nerve (n. trochlearis).
 - 7. its fibres passing to the superior oblique.
- VI. sixth nerve (n. abducens).
 - 6. its fibres passing to external rectus.
- C.A. carotid artery.
- E. vertical section through anterior part of eyeball; conjunctiva indicated by dotted line.

supra-orbital, the first of which supplies the conjunctiva of the upper eyelid, the skin of the eyebrow and of the inner part of the upper eyelid; the second (supra-orbital) supplies palpebral filaments to the upper lid, and is distributed to the skin of the forehead and scalp as far as the vertex, and to the pericranium covering the frontal and parietal bones.

The lacrimal branch (2) is seen giving off branches to the lacrimal gland (L.G.), and is continued onwards to supply the outer part of the skin and conjunctiva of the upper eyelid.

The nasal, or oculo-nasal, nerve (3) gives long ciliary nerves (3'') to the

ciliary muscle, iris, cornea, and conjunctiva; an infra-trochlear branch to the conjunctiva and integuments of the eyelids; a root (3'') (*radix longa ganglii ciliaris*) to the ophthalmic ganglion; besides terminal branches which supply the skin of the side of the nose and the pituitary mucous membrane.

In connection with the first division of the fifth nerve is seen the ophthalmic or ciliary ganglion. This ganglion is seen to receive three roots; its short

FIG. 83.

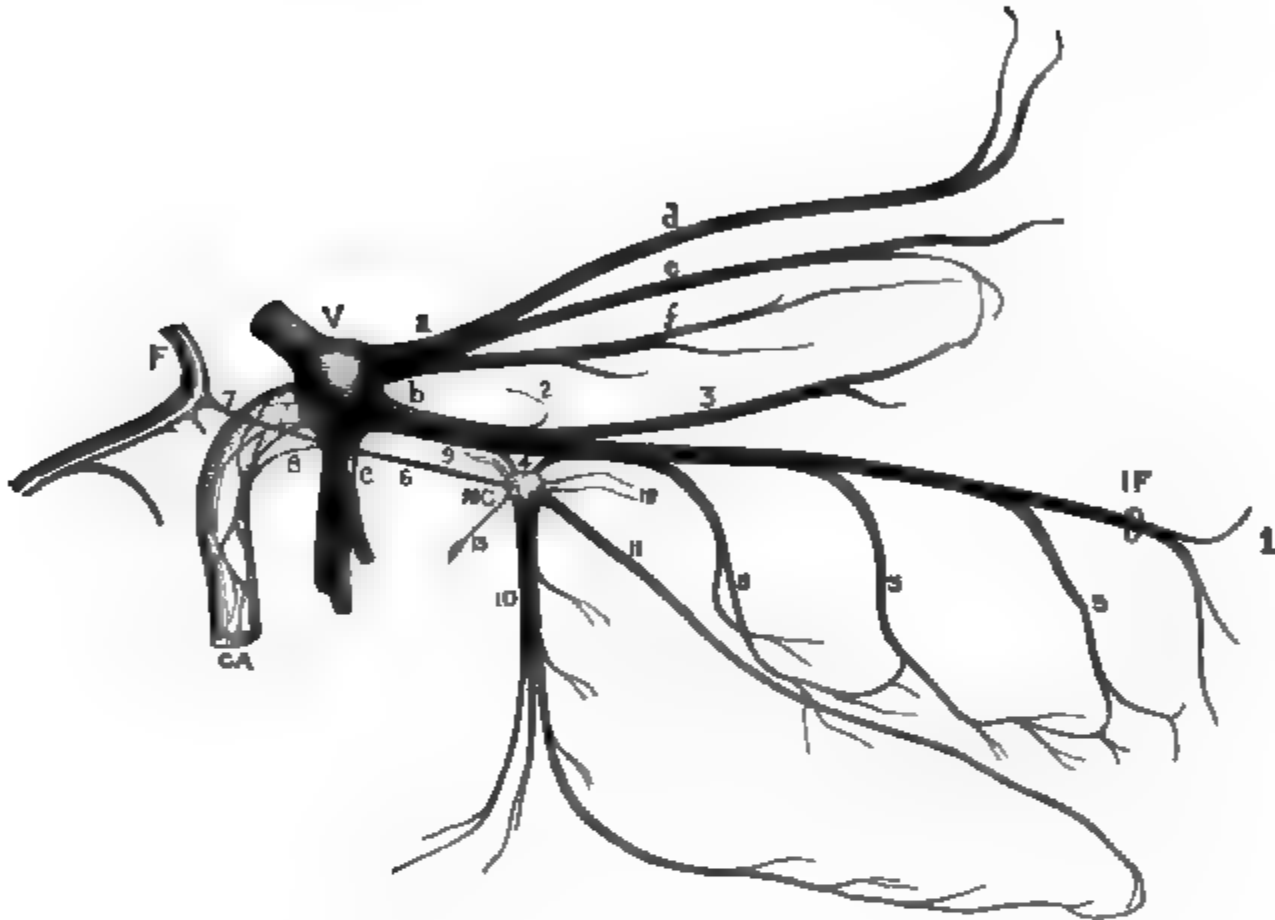


DIAGRAM OF THE SECOND (SUPERIOR MAXILLARY) DIVISION OF THE FIFTH NERVE, ITS CONNECTIONS AND CHIEF BRANCHES.

v placed over Gasserian ganglion.

a, first or ophthalmic division, with **d** its *frontal*, **e** its *lacrimal*, and **f** its *nasal* branches.

b, second or superior maxillary division, branches of which are marked as follows:—

1. its *terminal* branches, *nasal*, *labial*, and *palpebral*.

2. *recurrent* branch to the *dura mater*, and *middle meningeal artery*.

3. *orbital* branch.

4 is placed between the two *spheno-palatine* branches, which descend to Meckel's ganglion).

5. *dental* branches.

m o Meckel's ganglion.

6. the *Vidian* nerve (constituting the motor and sympathetic root of Meckel's ganglion).

7. the *great superficial petrosal* nerve, from the geniculate ganglion of the facial nerve, joining the *Vidian*.

8. the *sympathetic* branch from the plexus on the carotid artery, joining the *great superficial petrosal*, and forming with it the *Vidian* nerve.

9. ascending branches of Meckel's ganglion.

10. descending palatine branches.

11. *naso-palatine* branch.

12. *upper nasal* branches.

13. *pharyngeal* branch.

r facial nerve. **c a** carotid artery. **i f** infra-orbital foramen.

motor root (5) is derived from the third nerve; its long sensory root (8'') is derived from the nasal nerve, whilst the third root (shown by a dotted line in the figure) is derived from the cavernous plexus of the sympathetic. From the anterior part of the ganglion are seen proceeding the short ciliary nerves.

The function of the first division of the fifth is entirely sensory.

The second or superior maxillary division of the fifth nerve, with its chief branches and connections to other cranial nerves, is shown in fig. 33, where it is marked *b*. It is seen to give off the following branches: terminal infra-orbital branches (1), nasal, labial, and palpebral; of which the first supply the skin and mucous membrane of the nose; the second the skin and mucous membrane of the upper lip, and the third the skin and conjunctiva of the lower eyelid; a recurrent branch (2) to the dura mater and middle meningeal artery; an orbital branch (3) which divides into a *temporal* branch to a part of the skin of the temple, and a *malar* branch to the skin over the malar bone; dental branches, three in number, marked (5) which supply the teeth of the upper jaw; and spheno-palatine branches (4) which go to Meckel's ganglion (M G).

The ganglion connected with the second division of the fifth is termed Meckel's or the spheno-palatine ganglion. This ganglion receives the two roots (4) just mentioned from the superior maxillary nerve, and which doubtless contain only afferent fibres; it is also joined by a nerve, termed the Vidian (6), which when traced back is seen to be made up by the junction of the *large superficial petrosal* nerve (7), a branch of the facial nerve (F), and (8) the *carotid* or *sympathetic portion* of the Vidian nerve, from the *carotid plexus* of the sympathetic. The Vidian nerve gives off small nasal branches distributed to a limited region of the posterior nares, and to membrane covering the end of the Eustachian tube. The branches of distribution of Meckel's ganglion are seen to be: *ascending* branches (9) to the periosteum of the orbit; *descending palatine* branches (10) to the mucous membrane of the tonsils, gums, hard and soft palate, mucous membrane of nose, and supplying besides the *levator palati* and *azygos uvulae* muscles; a naso-palatine branch, or nerve of Cotunnus (11), upper nasal branches (12), a pharyngeal branch, the *pharyngeal nerve*, which is distributed to the lining membrane of the pharynx, close to the Eustachian tube.

The third division of the fifth, or inferior maxillary nerve is shown in fig. 34, p. 361, and in fig. 35, p. 364.

In the annexed figure (fig.) by *e* is represented the third division joined by *a* the smaller, motor, root of the fifth. By *F o* is indicated the *foramen ovale*, after passing through which the nerve divides into two divisions,—a smaller anterior division, marked *A*, which is mainly motor, supplying branches to the muscles of mastication (masseter, temporal, external, and internal pterygoid muscles), and a terminal sensory *long buccal branch* to the mucous membrane and skin of the cheek—a larger portion or division, marked *B*, which is mainly sensory, and which gives off the following branches: *auriculo-temporal* (4), to parotid gland, to skin of auricle, external meatus and temple, and the temporo-maxillary joint; gustatory or lingual nerve (1) which ends in the mucous membrane of the anterior two-thirds of the tongue, and which is joined by the chorda tympani (*c t*), a branch of the facial nerve which runs by its side and which gives to it some of its fibres, though the greater number pass to the submaxillary ganglion (*s g*) which is seen in close proximity to the gustatory, and which will be referred to more particularly below; *inferior dental* nerve (2) giving off twigs to the molar and bicuspid teeth (2'), an *incisor* branch to the canine and incisor teeth (2''), a *labial* or *mental* branch (2'') emerging from the *mental foramen* (*M F*) to supply the skin and mucous membrane of the lower lip; besides these the inferior dental (*n*) gives off the *mylohyoid* branch (3) which is distributed to the mylohyoid muscle and to the anterior belly of the digastric.

Two ganglia are connected with the third division of the fifth nerve, viz. the Otic ganglion, and the submaxillary ganglion.

The Otic ganglion, or ganglion of Arnold (see fig. 34 and fig. 35) receives a

root from the muscular nerve to the internal pterygoid, a root from the sensory auriculo-temporal nerve, a sympathetic root from the plexus on the middle meningeal artery, and a root from the *facial* and *glossopharyngeal* nerves, viz. the *small superficial petrosal* nerve (see fig. 34). The Otic ganglion gives off two branches, the first to the *tensor tympani*, the second to the *tensor palati*. The physiological importance of this little centre is, however, in all probability

FIG. 34.

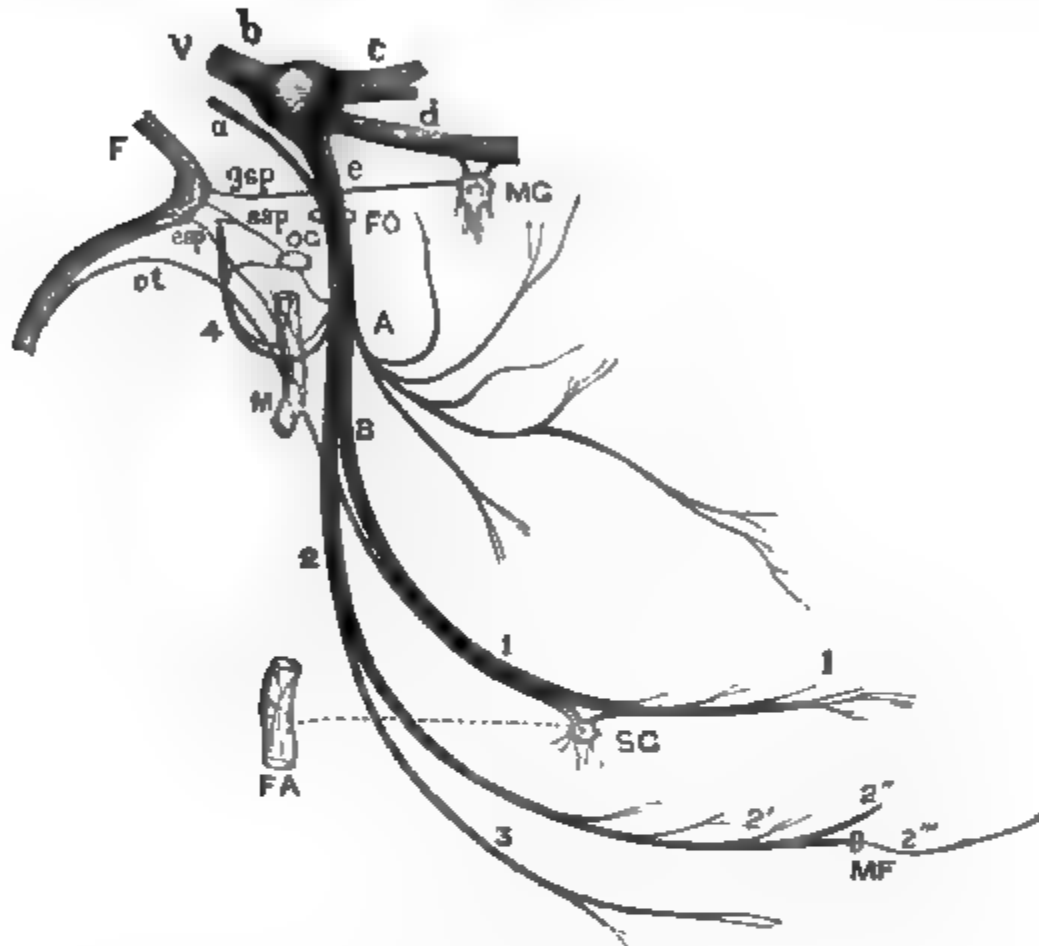


DIAGRAM OF THE THIRD (INFERIOR MAXILLARY) DIVISION OF THE FIFTH NERVE, ITS CONNECTIONS AND CHIEF BRANCHES.

- v fifth nerve. b its largest sensory root, with the Gasserian ganglion.
- a its smaller motor root joining e, the third division of the Gasserian ganglion, to form the inferior maxillary nerve.
- A anterior division of inferior maxillary nerve (mainly motor) supplying branches to the muscles of mastication, and a terminal buccal branch to the mucous membrane of the mouth.
- B posterior division (mainly sensory); its branches are marked,
 - 1. lingual nerve. 1' branches to the tongue.
 - 2. inferior dental nerve. 2' its twigs to the teeth. 2'' incisor branch. 2''' mental branch.
 - 3. mylo-hyoid branch to digastric and mylo-hyoid.
 - 4. auriculo-temporal nerve.
- f facial nerve. c t its *chorda tympani* branch, joining the lingual, and running to the submaxillary ganglion s o, of which it forms the motor root.
- o o otic ganglion.
- s s p small superficial petrosal nerve, connecting otic ganglion and facial nerve.
- m middle meningeal artery, from the plexus upon which sympathetic filaments pass to the otic ganglion.
- e s p external superficial petrosal nerve, connecting the plexus on the middle meningeal artery with the facial nerve.
- g s p great superficial petrosal nerve, connecting the facial with Meckel's ganglion.
- f a facial artery, from the plexus upon which sympathetic filaments pass to the submaxillary ganglion.
- f o foramen ovale. m f mental foramen.
- s o submaxillary ganglion.

much greater than one would conclude from the fact of its merely giving off these two small muscular branches, as it is probably through it that the fibres of the facial, contained in the small superficial petrosal nerve, make their way to the auriculo-temporal nerve, and thence to the parotid gland, for which they are most probably secretory. Further, it is probable that through the otic ganglion fibres of the glosso-pharyngeal, derived from its tympanic branch, make their way to the facial nerve.

The submaxillary ganglion, s & g, receives a sensory root from the lingual, a motor root from the chorda tympani, and a sympathetic root from the plexus surrounding the facial artery; it supplies fibres to the submaxillary and sublingual glands, which, in the case of the former, have been proved to contain vaso-constrictor, vaso-dilator, and secretory fibres.

Summary of the Functions of the Fifth Cerebral Nerve.—Its *sensory* fibres confer sensibility on nearly the whole of the head, and they serve the purposes of a large number of reflex acts. The regions of the head not supplied by the fifth are: portions of the pharynx, palate, and root of the tongue, which receive branches from the vagus and glosso-pharyngeal; the Eustachian tubes, tympanic cavity, and a part of the external auditory meatus and external ear which receives branches from the auricular branch of the vagus; and finally a portion of the back of the head [and the region of the parotid], which are supplied by the cervical spinal nerves. Some of the fibres of the fifth appear to belong to the nerves of taste [the lingual branch being, according to many, the nerve of the special sense of taste for the anterior two-thirds of the tongue, though it is not certain whether the fibres presiding over this function really originate in the fifth] (Chap. X.) Its *motor* fibres supply the muscles of mastication (temporal, masseter, mylo-hyoid, both pterygoids, and the anterior belly of the digastric), the tensor tympani, tensor palati, and probably also (Oehl) the dilatator iridis (Chap. X.) In addition, there run in the trigeminus vaso-motor fibres (probably of sympathetic origin) for the conjunctiva and iris. Finally, it contains *secretory* fibres for the lachrymal, parotid, and submaxillary glands.

Some ascribe to the fifth fibres of a trophic character, destined especially for the eyeball, since section of the fifth in the skull causes inflammation and degeneration of that organ. It has been asserted, however, that this result is to be attributed merely to loss of sensation which interferes with the protection of the eyeball from external influences; for inflammation has been said not to follow after section of the fifth if a sensitive protective surface be artificially placed before the eyeball, *e.g.* in rabbits by stitching in front of it the ear which is supplied by the cervical nerves (Snellen). This explanation has recently been doubted. In the first place, after paralysis of the facial no inflammatory changes follow, notwithstanding that the animal thus paralyzed is no longer able to protect its eye by closing the lid (Samuel). In the second place, after partial section of the trigeminal trunk—in which the innermost fibres have been left intact—no inflammation is noticed, notwithstanding the complete sensory paralysis which occurs, and that the eye remains unprotected by artificial means; while, on the other hand, the eye becomes inflamed very easily (if not artificially protected) if in partial section the innermost fibres have been destroyed, notwithstanding that sensation still remains (Meissner, Schiff). If, therefore, the preceding isolated statements should be confirmed, and if the influence of vaso-motor fibres

can be excluded, it will be necessary to resume the supposition of special 'trophic' fibres which course along the inner border of the trunk. The operation of these fibres is, as yet, quite unintelligible. The fifth is, moreover, said to contain trophic fibres for the cavity of the mouth, since section of that nerve occasions ulceration. The latter, however, depends upon the distortion of the lower jaw due to unilateral paralysis of masticatory muscles, whereby the teeth no longer meet, but press upon the mucous membrane opposite (Rollett).

Sixth Pair (N. abducens).

This is the motor nerve for the external rectus muscle of the eyeball (abducens).

Then abducens receives fibres from the cervical portion of the sympathetic; so that the external rectus receives fibres from the cilio-spinal region of the spinal cord in addition to those contained in the Sixth Pair (Chap. XI.)

[When the sixth nerve is paralyzed, there occurs well-marked internal strabismus.]

Seventh Pair (Facial N. Portio dura of the Seventh Cranial Nerve of Willis).

[The relations of the facial nerve to other cranial nerves, and the chief branches which it gives, are shown in fig. 35. The facial nerve F is seen contiguous to the auditory nerve A. At 1 is seen its geniculate ganglion where it is joined by the *great superficial petrosal* (g s p), the *small superficial petrosal* (s s p), and the *external superficial petrosal* (e s p) nerves. The first establishes a communication between Meckel's ganglion and the facial; the second between the Otic ganglion and the facial, and probably between the glosso-pharyngeal and the facial; the third establishes a communication between the sympathetic plexus surrounding the middle meningeal artery and the facial. (For the relations of the *tympanic branch* of the glosso-pharyngeal to the seventh nerve, see fig. 36.) Of these branches, the first, the great superficial petrosal—which joins the Vidian—in all probability serves the purpose of carrying efferent fibres from the seventh to Meckel's ganglion; the small superficial petrosal is, however, in all probability the medium for the introduction of fibres from the glosso-pharyngeal, and possibly also from the fifth into the facial; whilst the external superficial petrosal most probably adds sympathetic (*vaso-constrictor* and *vaso-dilator*?) fibres to those already present in the facial nerve.

The facial nerve is seen to give off the following branches: a *branch* to the *stapedius* muscle (3); the *chorda tympani* (2) which joins the lingual branch of the inferior maxillary, accompanying it as far as the submaxillary ganglion (s g), furnishing in its course fibres to the lingual nerve (Prevost), but chiefly being distributed to the *submaxillary ganglion*; *communicating filaments* to pneumogastric (4); *posterior auricular* branch (5) to the occipital belly of the *occipito-frontalis* and to the *retrahens aurem*; and the *digastric* branch (6), supplying the posterior belly of the digastric and the stylo-hyoid muscle, and which often communicates with the glosso-pharyngeal. Having given off these branches, the nerve divides into its *temporo-facial* (T F) and *cervico-facial* divisions (C F), which are mainly distributed to the muscles of expression, giving also branches to the buccinator muscle, the platysma myoides, and the muscles of the scalp and external ear.

FIG. 85.

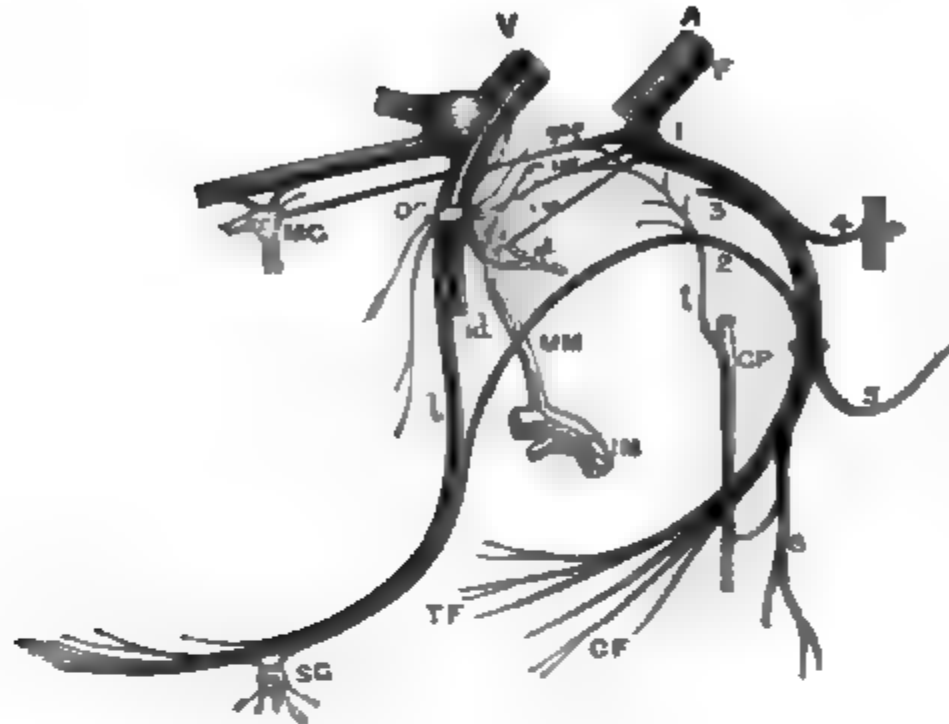


DIAGRAM OF THE FACIAL NERVE, ITS CONNECTIONS AND BRANCHES.

V the facial nerve.

A auditory nerve.

1. the geniculate ganglion.

gsp great superficial petrosal nerve connecting the facial and Meckel's ganglion.

ssp small superficial petrosal connecting the facial nerve with the Otic ganglion and with the tympanic branch of the glossopharyngeal.

esp external superficial petrosal connecting the facial with the plexus on the middle meningeal artery.

2. chorda tympani, joining lingual nerve.

3. nerve to the stapedius muscle.

4. communicating branch with the ganglion of the root of the vagus.

5. posterior auricular nerve.

6. branch to the stylo-hyoid and digastric muscles.

TF temporo-facial division } to muscles of expression.

CF cervico-facial division }

v fifth nerve. at auriculo-temporal branch.

id inferior dental nerve.

l lingual nerve.

MG Meckel's ganglion.

OG Otic ganglion.

SG submaxillary ganglion.

IM internal maxillary artery.

MM middle meningeal artery.

P pneumogastric nerve.

G glossopharyngeal nerve.

t its tympanic branch (nerve of Jacobson).

Summary of the Functions of the Facial Nerve.

This nerve contains almost exclusively efferent (motor and secretory) fibres. Whenever its branches possess sensory functions these are due to the presence of fibres from the fifth, and, to a small extent, of fibres from the vagus [and perhaps of the glossopharyngeal]; the latter surmises account for the fact that paralysis of the fifth does not cause complete loss of sensibility. According

to recent researches the chorda tympani contains gustatory and vaso-dilator fibres for the anterior part of the tongue. Its *motor* fibres supply all the superficial muscles of the head—the ‘muscles of expression,’ the muscles of the external ear, the stylo-hyoid muscle, the posterior belly of the digastric, the levator palati, the azygos uvulæ, the stapedius, and finally the platysma myoides. Its *secretory* fibres act upon the salivary glands.

Paralysis of the facial of one side causes contraction of the face towards the opposite side. This is due to the fact that after contraction of the face the elasticity of the paralyzed muscles is not sufficient to stretch out the muscles of the opposite side to their previous length. [There is a loss of all expression on the palsied side. The eye, in consequence of the paralysis of the *orbicularis palpebrarum*, remains wide open, unwinking; and the tears no longer spread over the eyeball and are not conducted to the puncta lachrymalia, but flow over the cheek; whilst the eye, no longer protected from the contact of foreign particles, often becomes irritated and inflamed.

The buccinator being completely paralyzed the cheek is puffed out at each expiration; if an attempt be made to whistle the attempt fails, and the flaccid cheek on the affected side contrasts with the distension of the opposite side. The muscles of the lips being paralyzed as well as the buccinator, particles of food make their way between the teeth and the cheek and there accumulate. The movements of the nostril cease; and, in consequence of the impossibility to draw air into the nostril by sniffing, the sense of smell becomes less acute than normal.

In addition to the above there are changes in the form of the soft palate, and affections of hearing and taste which require careful examination. According to most writers on facial paralysis, a change in the soft palate is to be noted in this affection; the description of the change has however in general been inaccurate. From the very careful observations of Sanders,¹ which the editor had the opportunity of witnessing, there occurs, in lesion of the facial nerve, a vertical relaxation or lowering of the half of the velum palati corresponding to the affected side, with diminished height and curvature of the *posterior palatine arch* on the paralyzed side. This condition is due to the paralysis of the *levator palati*. In addition, there is usually a drawing of the uvula towards the paralyzed side (not, as most medical writers have described, towards the healthy side); this is probably due to the palato-pharyngeus which is unaffected, and which is no longer antagonized by the levator palati, exerting a greater effect upon the uvula on the affected side than can be exerted by the palato-pharyngeus on the unparalyzed side. There are facts which show that, in addition to the levator palati, the only muscle of the soft palate which is affected in paralysis of the seventh is the *azygos uvulæ*, so that we may conclude with safety that the levator palati and the azygos uvulæ are the only palatine muscles receiving efferent fibres from the seventh.

Affections of hearing are very common in paralysis of the seventh; these are sometimes due to participation of the eighth nerve in the morbid process which gives rise to the palsy of the contiguous nerve; it is most probable, however, that there is an affection of hearing which is an essential phenomenon of facial palsy, and which is dependent upon the paralysis of the *nerve* to the *stapedius*.²

Finally, in all cases of paralysis of the seventh nerve there is an affection of the sense of taste in the anterior portion of the tongue; in certain cases this

¹ W. R. Sanders, M.D. ‘Vertical Hemiplegia of the Palate in Facial Palsy,’ *Edinburgh Medical Journal*, August 1865.

² See the case of Professor Roux, quoted by Longet, *Traité de Physiologie*, 8rd ed. (1869), T. iii. p. 578.

loss of the sense of taste is complete, though common sensibility persists.¹ The most probable explanation of this phenomenon appears to be that the chorda tympani contains the fibres which minister to the special sense of taste in the anterior two-thirds of the tongue. This subject will be discussed more completely under the heading of 'The Organ of Taste.']

Eighth Pair (Auditory N. Portio mollis of the Seventh Cranial Nerve of Willis).

This is the only nerve connected with the special sense of hearing. Even stimulation of this nerve occasions an auditory sensation, and its section is followed by deafness; it is also engaged in conducting other than auditory impulses from the semicircular canals (see Chap. X.)

Ninth Pair (Glosso-pharyngeal N.—Part of the Eighth Cranial Nerve of Willis).

[In fig. 36 is shown, diagrammatically, the glosso-pharyngeal nerve (G) and its relations to the facial (F), pneumogastric (P), and sympathetic (S) nerves. Upon the trunk of the nerve is seen first the *jugular ganglion* (J G) and then the *petrous ganglion* (P G), communicating with the *ganglion of the root* of the pneumogastric, and with the *superior cervical ganglion* of the sympathetic. From the petrous ganglion is given off the *tympanic branch or nerve of Jacobson* (1), the branches of which are: filaments to plexus on carotid artery (2): branch to *Eustachian tube* (3): branch to *fenestra rotunda* (4): branch to *fenestra ovalis* (5): a twig of union with the *small superficial petrosal nerve* (6): a twig of union with the *great superficial petrosal nerve* (7). Between the two latter branches the fibres of the glosso-pharyngeal may make their way to the *Otic ganglion*, to *Meckel's ganglion*, and to the *facial nerve*.

Following down the trunk of the nerve from the *petrous ganglion*, it is seen to give off: *pharyngeal branches* (8), which unite with branches of the pneumogastric and sympathetic to form the *pharyngeal plexus* (see also fig. 37), the fibres of the glosso-pharyngeal being distributed to the mucous membrane of the pharynx: *muscular branches* (9) to the *stylo-pharyngeus*, and to the *constrictors* of the *pharynx* (?): *tonsillitic branches* (10) forming the plexus-like arrangement called the *circulus tonsillaris*, whence fibres pass to the soft palate and *isthmus* of the fauces: and lastly, *lingual branches*, which are distributed to the mucous membrane covering the base of the tongue, where many of the fibres enter the *circumvallate papillæ*.]

The glosso-pharyngeal is a mixed nerve which, however, only contains a few motor fibres for the following muscles, *levator palati*, *azygos uvulæ*, *middle constrictor of the pharynx*, and *stylo-pharyngeus*.

[In the opinion of the editor, for the reasons stated at p. 365, the two muscles first mentioned are supplied by the facial nerve (see also Quain's 'Anatomy,' Turner²).]

The remaining fibres are afferent, and minister in part to common sensibility, but chiefly to the sense of taste in the soft palate and the root of the tongue.

¹ A. Davidson, M.D., 'On the Sense of Taste and its Relation to Facial Paralysis and Anæsthesia.'

² Quain's *Anatomy*, 8th ed. (1876), vol. i. p. 290.

³ Turner, *An Introduction to Human Anatomy* (1875), part i. p. 805.

[Considerable doubt surrounds all statements concerning the motor functions of the glosso-pharyngeal, the statements of different observers being remarkably discordant. There is strong reason for believing that any motor fibres which the nerve may contain, as those said to be distributed to the *stylo-pharyngeus*, are derived from the facial n.]

FIG. 86.



DIAGRAM OF GLOSSO-PHARYNGEAL NERVE, ITS CONNECTIONS AND BRANCHES.

- G P glosso-pharyngeal nerve. J G its jugular ganglion. P G its petrous ganglion.
 1. tympanic branch, or nerve of Jacobson, the branches of which are as follows:—
 2. filaments to plexus on carotid artery; 3, to Eustachian tube; 4, to fenestra rotunda;
 5, to fenestra ovalis.
 6. twig of union with small superficial petrosal n.
 7. twig of union with great superficial petrosal n.
 8. pharyngeal branches of glosso-pharyngeal n.
 9. muscular branches to stylo-pharyngeus and constrictors (?)
 10. tonsillitic branches.
 11. terminal lingual branches.
 S pneumogastric nerve, from the ganglion of the root of which branches pass to the petrous ganglion.
 J superior cervical ganglion with an ascending branch to the petrous ganglion.
 M G Meckel's ganglion. O G Otic ganglion. F facial nerve. CA carotid artery.

Tenth and Eleventh Pairs (N. Vagus or Par Vagum and Spinal Accessory Nerve; Divisions of the Eighth Cerebral Nerve of Willis).

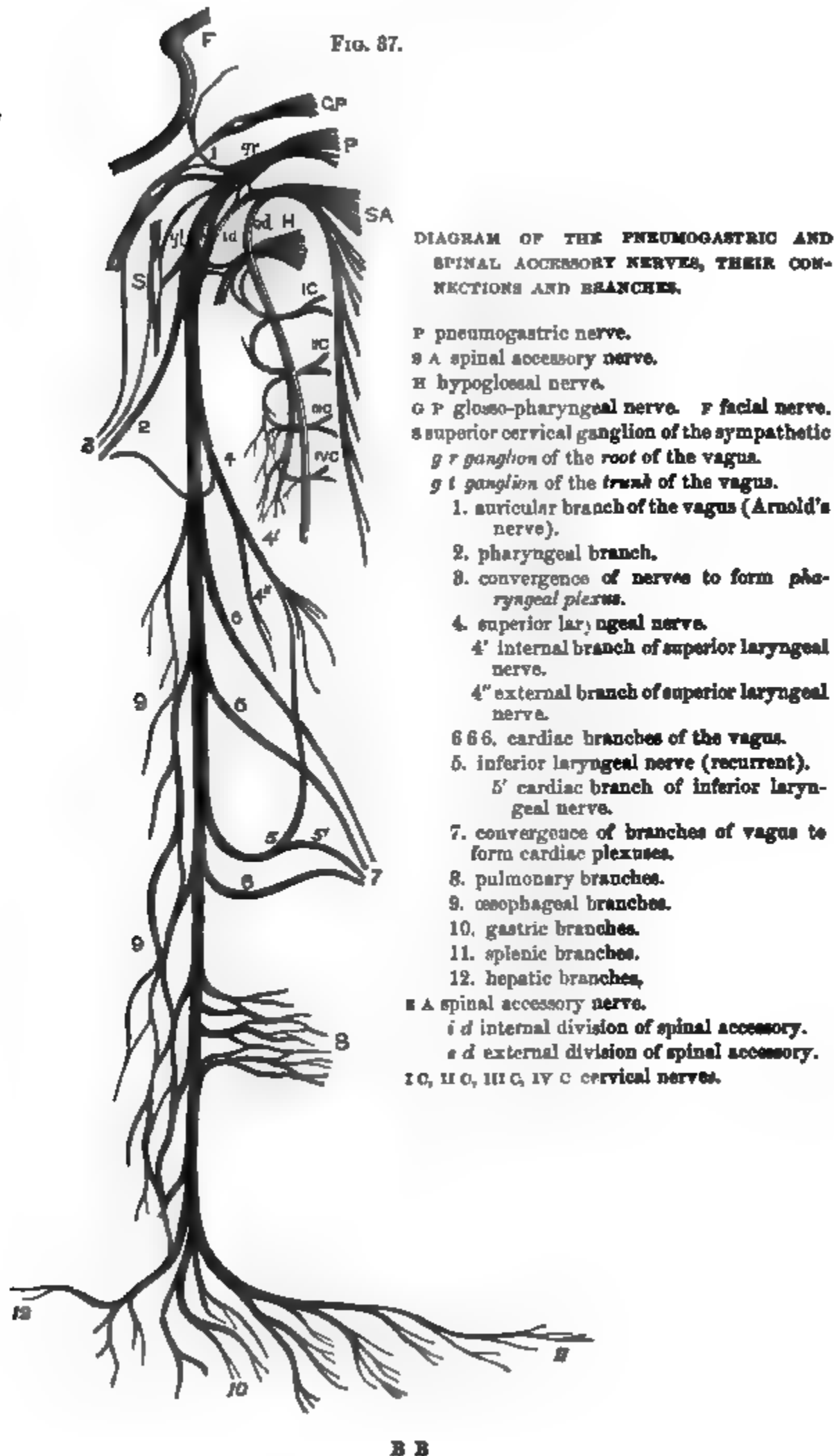
Together these form a mixed nerve. It has been maintained (Longet) that these two nerves are to be regarded as two roots, of which one (the vagus) contains the afferent, whilst the other (the spinal accessory), whose inner or anterior branch unites with the vagus of descriptive anatomy, contains the efferent fibres. The vagus, however, at its origin, contains motor fibres for the larynx, pharynx, and œsophagus (Van Kempen).

[In fig. 37 is seen a diagrammatic representation of the vagus and spinal accessory nerves, and their relation to other nerves.

F indicates the *facial* nerve, G R the *glosso-pharyngeal* nerve, P the *pneumogastric* nerve, H the *hypoglossal* nerve, S A the *spinal accessory* nerve, whilst I C, II C, III C, and IV C indicate *cervical spinal* nerves.

Considering first the *pneumogastric*, we observe at the commencement of its course the *ganglion* of the *root* (*g r*). This ganglion is seen to receive filaments from the *internal division* of the *spinal accessory* (*i d*); it is connected besides with the *petrous ganglion* of the *glosso-pharyngeal*, and with an ascending branch from the upper cervical ganglion of the *sympathetic* (*s*). From the ganglion of the root the *auricular branch* (Arnold's nerve) (1) is given off, which, joining with a twig from the *glosso-pharyngeal*, and the *facial*, is distributed to the skin covering the back of the external ear. Below the first-mentioned ganglion is seen the *ganglion* of the *trunk* (*g t*), which does not include all the fibres of the nerve, as, for instance, the fibres derived from the *internal division* of the *spinal accessory*. Connecting branches extend between the ganglion of the trunk and the *hypoglossal*, *spinal*, and *sympathetic* nerves. From the ganglion of the trunk are given off: the *pharyngeal branch* (2), which, meeting branches from the *sympathetic glosso-pharyngeal* and *superior laryngeal* nerves, forms the *pharyngeal plexus* (3), whence fibres proceed to the muscular structures and the mucous membrane of the pharynx; it is the fibres from the vagus which doubtless supply the former: the *superior laryngeal* nerve (4), dividing into an *internal branch* (4'), to the mucous membrane of the larynx and epiglottis, to the arytenoid muscle, which it supplies in part, and which communicates with a branch of the *recurrent laryngeal*, and an *external branch* (4''), which supplies the crico-thyroid muscle. The trunk of the *pneumogastric* gives off the following branches: *cardiac branches* (6), which arise partly in the neck and partly in the chest, and join the *cardiac plexus* (7). (The *recurrent laryngeal* also furnishes cardiac branches (5')): the *recurrent laryngeal* branch (5), which winds round from the thorax and is distributed to the larynx, supplying its intrinsic muscles, with the exception of the *crico-thyroid*, filaments being given off previously to join the *cardiac plexus*: *œsophageal branches* (9), which form the *œsophageal plexus*, which supplies both muscles and mucous membrane of the œsophagus: *pulmonary branches* (8), which, with the *sympathetic*, form the *anterior and posterior pulmonary plexuses*: *gastric branches* (10), supplying the stomach, and giving branches to the *solar plexus*: *splenic branches* (11), joining the *splenic plexus* (only from right vagus): *hepatic branches* (12), joining the *hepatic plexus* (only from left vagus).

The *Spinal Accessory Nerve* (S A) is seen to divide into two divisions, of which the *internal* (*i d*) has already been referred to as joining the vagus,



furnishing filaments to the *ganglion* of the root, and afterwards blending with the trunk of the nerve; the *external division* (*ed*) supplies the trapezius and sterno-mastoid muscles, and forms anastomoses with the third and fourth cervical nerves.

Summary of the Functions of the Pneumogastric and Spinal Accessory Nerves.

The centrifugal fibres, so far as is known, are the following :

a. Motor fibres. 1. For the muscles of the pharynx. 2. For the muscles of the larynx, contained for the most part, in the n. laryngeus inferior or recurrent laryngeal. The n. laryngeus superior supplies a branch for the crico-thyroid muscle: this statement has, however, been lately denied. 3. For the muscles of the bronchi: this is, however, doubtful. 4. For the œsophagus; after section of both vagi food which is swallowed no longer enters the stomach, while after section of the accessories no such result follows. 5. For the stomach. 6. According to some writers, for the small and large intestine and for the uterus. 7. For the sterno-cleido-mastoid and trapezius muscles, the fibres being situated in the outer or posterior branch of the spinal accessory of descriptive anatomy.

b. Regulating—inhibitory—fibres for the heart (Ed. Weber,¹ Budge).

c. Secretory fibres. 1. For the glands of the gastric mucous membrane, &c.: this fact has not been conclusively proved, and has lately been contested. 2. For the kidneys (Bernard²), since irritation of the vagus at the cardia is said to increase the urinary secretion, producing simultaneously arterialization of the venous blood (?)

d. Vaso-motor fibres for the vessels of the abdomen (Rossbach and Quillhorst); the statements concerning the fibres for the vessels of the lungs have not been confirmed.

The centripetal fibres are the following :

a. Sensory fibres supplying, in all probability: 1. The whole respiratory apparatus. 2. The digestive apparatus from the velum palati to the pylorus. 3. The heart.

b. Regulating fibres: 1. Accelerating for the inspiratory centre, arising probably in the lungs. 2. Inhibitory for the same centre (Rosenthal³). The distribution of these accelerating and inhibitory fibres among the branches of the vagus has been described on p. 201. 3. Stimulant for the cardiac inhibitory centres (Donders). 4. Stimulant for the vaso-motor centre ('pressor fibres'), especially in the superior laryngeal branch (Aubert and Roever⁴). 5. inhibi-

¹ E. Weber in Wagner's *Handwörterbuch d. Phys.* Vol. iii. p. 81.

² Bernard, *Leçons sur les Liquides de l'Organisme.* Vol. ii. p. 171.

³ Rosenthal, *Die Athembewegungen.* 1862.—*Archiv f. Anat. u. Phys.* 1864, p. 456; 1865, p. 191; 1870, p. 428.

⁴ 'Aubert and Roever,' *Pflüger's Archiv.* Vol. i. p. 224.

tory for the same centre, which in many animals run in a special branch, the *Ramus depressor nervi vagi* (Ludwig and Cyon¹). 6. Stimulant for the salivary secretion, arising probably from the stomach (though this is doubtful: consult p. 130 *et sq.*). 7. Inhibitory for the pancreatic secretion (Ludwig and N. O. Bernstein²). 8. Stimulant for the sugar-formation in the liver, *i.e.* fibres, the centripetal irritation of which calls into reflex activity the nerves which lead to the formation of sugar; these fibres have their peripheral terminations in the thorax, possibly in the lungs (Bernard).

The results of experimental section and irritation of the vagus and accessory, which have served to determine the various series of fibres contained in those nerves will now be gathered into a *résumé*.

1. Section of the spinal accessory above its point of union with the vagus (or, as is the usual plan, removal of the accessorius-roots from the cord), paralyzes all the muscles dependent upon the vago-accessorius for their nerve-supply: according to some, the laryngeal muscles (van Kempen, Navratil) are not affected, and the power of swallowing is not entirely lost. In addition section of the spinal accessory causes acceleration of the heart's action, while stimulation produces slowing (Waller, Heidenhain). Unilateral paralysis of the external portion of the accessorius causes a twisting of the head.

2. Irritation of the vagus above the point of union with the spinal accessory causes, among other things, contractions in larynx, pharynx, and œsophagus.

3. Section of the vagus-trunk in the neck causes (*a*) paralysis of laryngeal muscles, and, in consequence, when both vagi are divided, inaction of the vocal cords, loss of voice and passage of portions of food into the lungs, whereby fatal pneumonia is induced; (*b*) quickening of the heart's action; (*c*) slowing of the movements of inspiration; (*d*) prevention of those reflex acts which stimulations applied to larynx, pharynx, and stomach, normally induce; (*e*) prevention of the last act in the operation of swallowing, so that the œsophagus becomes filled with food; (*f*) interruption of the sugar-formation in the liver (?)

4. Irritation of the peripheral portion of the divided vagus in the neck causes (*a*) spasms of the glottis or contraction of the laryngeal muscles, which is also induced by irritation of the peripheral end of the inferior laryngeal nerve; (*b*) slowing of the heart's action, and finally stand-still of that organ in diastole; (*c*) contraction (so it is said) of the smooth muscles of the bronchi,³ thus narrowing their lumen somewhat; this has, however, been frequently denied, by Donders, Wintrich, Rosenthal and Rügenberg, but has been again supported recently by Schiff and Bert⁴; (*d*) contraction of stomach, intestine (?), uterus (?), &c.; (*e*) increased renal secretion (?)

5. Irritation of the central portion of the divided vagus in the neck causes (*a*) quickening of inspiratory movements, which proceeds even to inspiratory tetanus; occasionally, however, an opposite result follows (p. 201); (*b*) increased sugar-formation (?); (*c*) increased salivary secretion (?); (*d*) diminished pancreatic secretion; (*e*) diminished blood-pressure if stimulation be applied above the point of union of depressor and vagus; (*f*) slowing of the heart's beat when the other vagus is intact.

¹ E. Cyon and C. Ludwig, 'Die Reflexe eines der sensiblen Nerven des Herzens auf die Motorischen der Blutgefäße,' *Ber. d. K. Sächs. Gesell. zu Leipzig*. 1866, p. 307.

² Bernstein, 'Zur Physiologie der Bauchspeicheldrüse,' *Ber. d. K. Sächs. Gesellsch. d. Wissensch. zu Leipzig*. 1869, p. 103.

³ Williams, 'Report of Experiments on the Physiology of the Lungs and Air-tubes,' *Reports of the British Assoc.* 1840 (Glasgow Meeting), p. 411.

⁴ Bert, *Leçons sur la Physiologie comparée de la Respiration*. Leçon xxi. p. 375.

6. Section or paralysis of the inferior laryngeal nerve paralyzes the laryngeal muscles, causing the same phenomena as section of the vagus in the neck (see 3 *a*); aneurisms of the aortic arch sometimes press upon the left inferior laryngeal nerve, thus producing paralysis of the left vocal cord.

7. Section of the superior laryngeal nerve causes a slight slowing of inspiration (Sklarek), on account of the motor fibres for the larynx, and especially for the crico-thyroid muscle, which it contains. Nawratil has recently denied that the crico-thyroid muscle receives motor supply from this nerve.

8. Irritation of the central portion of the divided superior laryngeal nerve causes (*a*) slowing of inspiration which proceeds to complete cessation of the respiratory movements (Rosenthal); (*b*) increased blood-pressure by inducing contraction of the arteries.

9. Irritation of the central portion of the divided depressor branch of the vagus causes dilatation of all the arteries and, in consequence, a fall of blood-pressure (Cyon and Ludwig).

The irritability of the fibres of the vagus or, more correctly, of the end-organs of the fibres, varies with the fibre.

On irritation of the peripheral portion of a divided vagus, a stronger stimulus is needed to produce slowing of the heart than is necessary to produce contraction of the laryngeal muscles (Rutherford¹). During irritation of the central portion the fibres which cause quickening of respiration are sooner exhausted than those which cause slowing (Burkart). The inhibitory fibres for the heart are sometimes very unequally divided between the two vagi.

Twelfth Pair (Hypoglossal Nerve, Ninth Cerebral Nerve of Willis).

[In fig. 38 the hypoglossal nerve is shown with its relations to the pneumogastric, sympathetic, and cervical nerves.

Close to its origin the nerve is seen to send filaments (1) to the ganglion of the trunk of the pneumogastric; it afterwards receives filaments from the superior cervical ganglion of the sympathetic, and from the loop which connects the two first cervical nerves.

The trunk of the nerve gives off the *descendens noni* (4) ('*descendens noni*') which unites with a branch from the second and third cervical nerves (5) to form the *ansa hypoglossi*, from which branches are given to the omohyoid, sterno-hyoid, and thyro-hyoid muscles.

After giving off the *descendens noni*, the hypoglossal gives off a branch to the *thyro-hyoid* muscle (6); terminal branches (7), to the styloglossus, hyoglossus, genio-hyoid, genio-hyoglossus muscles, and also to the intrinsic muscles of the tongue.

Summary of Functions of Hypoglossal Nerve.

This nerve is the motor nerve for all the muscles of the tongue, and, therefore, also a motor nerve concerned in speech. In addition, it supplies the muscles connected with the os hyoides. It receives sensory fibres through its ramus descendens from the first cervical nerve, in consequence of which the tongue retains a certain amount of sensibility even after section of the fifth.

¹ Rutherford, 'Influence of the Vagus upon the Vascular System,' *Transactions of the Royal Society of Edinburgh*, 1869, 70.

FIG. 88.

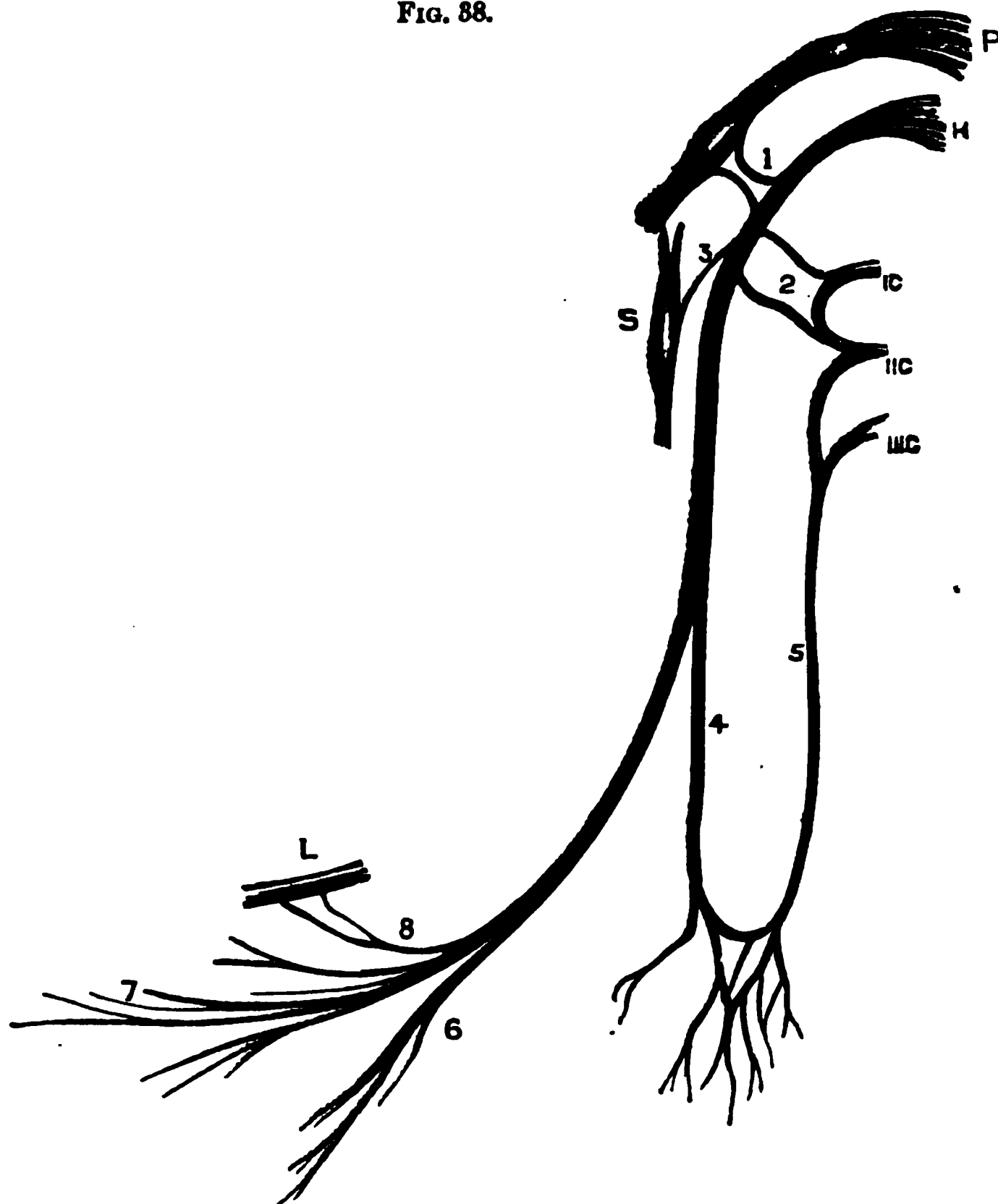


DIAGRAM OF THE HYPOGLOSSAL NERVE, ITS CONNECTIONS AND BRANCHES.

- H. hypoglossal nerve. P. pneumogastric nerve.
 S. superior cervical ganglion of the sympathetic. L. lingual nerve.
 I C, II C, III C. the three upper cervical nerves.
1. communicating branches from hypoglossal to ganglion of the trunk of the vagus.
 2. connecting filaments with the loop of first and second cervical nerves.
 3. branch to the sympathetic.
 4. descendens noni.
 5. branch from second and third cervical nerves (communicantes noni).
 6. branch to thyro-hyoid.
 7. terminal muscular branches.
 8. communicating branch to lingual branch of the fifth.

III. Sympathetic Nerves.

The consideration of the sympathetic nerves cannot well be separated from that of the sympathetic central organs, which will be found in Chap. XI., where, also, the reasons for such combined treatment are given at length.

CHAPTER X.

THE PERIPHERAL END-ORGANS OF NERVES.

IN discussing the organs engaged in secretion and motion the little which is known concerning the peripheral termination of *centrifugal* nerves has been referred to. The peripheral organs of *centripetal* nerves have in great part been accurately investigated. Many of these are in connection with contrivances which serve to transmit in a suitable manner to the end-organs the influences of the external medium, such as light, sound, heat, pressure, &c., which are capable of exciting nerves. For this purpose there exist organs which are composed both of conducting arrangements and end-organs of nerves, and which are called *Organs of the Senses*.

As the physiology of the conducting arrangements cannot be separated from that of the end-organs, the whole of the physiology of the Organs of the Senses will be here treated of.

I. THE ORGAN OF SIGHT.

In the organ of sight, the eye, the end-organs of the nerves terminate in a spherically-curved membrane (the *retina*); the luminous impressions capable of exciting the sense of sight fall upon this surface. The rays of light which enter the eye are projected by means of a system of different refractive media upon the retina, in such a manner that a diminished, inverted, and *real* image of the objects seen is formed upon it, just as in a camera obscura.

Schema of the Eye.

The refractive media of the eye, in the order in which they are traversed by the rays of light which fall upon them, are the following: 1. The cornea. 2. The aqueous humour. 3. The lens with its capsule. 4. The vitreous body. Four separating surfaces (refracting surfaces) correspond to these media: 1. A surface between the air and the substance of the cornea (anterior surface of the cornea). 2. A surface between the cornea and the aqueous humour (posterior surface of the cornea), &c. In order to be able to follow the paths of luminous rays which pass through the eye to the retina, the following data must be known: 1. The refractive indices

of all the media. 2. The forms of all the refracting surfaces. 3. The distances of these from one another and from the surface upon which the image is projected (retina).

The crystalline lens is not a simple refracting medium; its consistence and its power of refraction increase from the exterior to the interior, its solid nucleus, which is of very small radius of curvature, refracting light most powerfully.

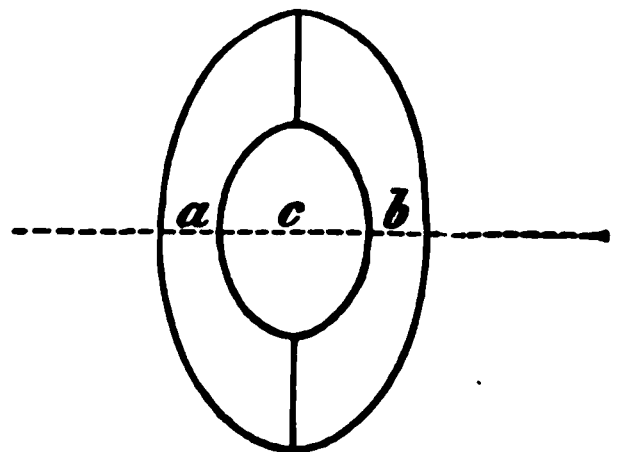
The annexed diagram, fig. 39, which represents in a simplified manner the structure of the lens, shows that it may be looked upon as made up of a powerful convex lens *c* and of two concave lenses *a* and *b*.

The latter neutralize to a certain extent the action of *c*, and they do so the less the smaller their refractive index. Inasmuch as *a* and *b* possess a smaller index of refraction than *c*, the action of the lens as a whole is greater than it would be if they had the same index of refraction as *c*, *i.e.*

it is greater than would be the case were the lens composed of homogeneous matter having the same index of refraction as the nucleus. The focal distance of the lens being determined by experiment, and its shape being known, the so-called total index of refraction of the lens may be calculated, *i.e.* the index of refraction which the lens would possess, were it homogeneous. According to what was said previously, it follows that the index thus calculated is greater than that of the nucleus.

The optical problems connected with the eye are much simplified by the fact that the cornea is a membrane the surfaces of which are parallel, and which limits anteriorly and posteriorly fluids which possess approximately the same index of refraction (in front is the lachrymal fluid which moistens it, behind the aqueous humour); such a body (like a plate of glass the surfaces of which are in contact with air, *e.g.* a window-pane or a watch-glass) cannot give a new direction to a ray of light which traverses it, but can only deviate it slightly in a direction parallel to itself. The cornea itself may therefore be entirely neglected, and we may reason as if the aqueous humour extended to the anterior surface of the cornea. There remain, therefore, only three refracting media to be taken into account—the *aqueous humour*, the *lens*, and the *vitreous body*, in addition to three refracting surfaces, viz. the *anterior surface of the cornea* and the *anterior and posterior surfaces of the crystalline lens*. The centres of curvature of these three surfaces lie in one straight line—the *optic axis*.¹

FIG. 39.



¹ When examined under water the action of the anterior surface of the cornea also ceases, so that the eye under these circumstances possesses but two refracting surfaces. The consequences of this will be seen further on.

The following data apply to the eye when at rest (*i.e.* when not *accommodated* for distance) (Listing ¹).

(*a.*) The refracting surfaces are spherical surfaces, the radii of which have the following measurements :

1. The anterior surface of the cornea about 8^{mm}
2. The anterior surface of the lens „ 10^{mm}
3. The posterior surfaces of the lens „ 6^{mm}

(*b.*) The distances between these refracting surfaces are—

- | | | | | | | |
|-------------------------------|---|---|---|---|-------|------------------|
| from 1 to 2 | . | . | . | . | about | 4 ^{mm} |
| „ 2 to 3 ('axis of the lens') | . | | | | „ | 4 ^{mm} |
| „ 3 to the retina | . | . | . | | „ | 13 ^{mm} |

(*c.*) The *indices of refraction* are (that of air being taken as 1) for the aqueous humour $\frac{103}{77}$
 for the lens (*total*) . . . = $\frac{16}{11}$
 for the vitreous body . . . = $\frac{103}{77}$

The results of the most accurate of these determinations (Brewster,² the two Krauses,³ Helmholtz⁴) cannot here find a place; only the methods which have been employed in making them can be shortly indicated. The refractive indices of the fluid media have been determined by well-known optical methods in eyes removed from the body; the total refractive index of the lens is calculated from its empirically determined focal distance and from its external form. The determination of the radii of curvature must, when possible, be determined in the living eye, as the forms undergo various changes (see below). This determination is made by the following very exact method, which is specially of importance in ascertaining exactly the changes which occur during accommodation (Helmholtz⁵). According to simple geometrical principles the radius of a spherical surface may be calculated by placing a body of linear form and of known length at a measured distance from it, and measuring the image of the body reflected at the spherical surface. These measurements are effected in the following manner: the corneal image, which we shall suppose to be horizontal, is observed through a thick glass plate. This plate is divided horizontally into two halves, which are movable around a common vertical axis. So long as the rays of light pass perpendicularly through the glass plate, the reflected image appears unchanged; if now the two glass plates are turned around their axis, but from opposite sides (so that looked at from above they appear crossed), each plate is struck obliquely by the rays, and in consequence the image is displaced in a horizontal direction. The two plates displace the image in opposite directions, and there appear *two* images; if now the plates have been turned to

¹ Listing, art. 'Dioptrik des Auges,' in Wagner's *Handwörterbuch d. Physiologie*. Vol. iv. p. 451.

² Brewster, *Edin. Phil. Journal*. 1819, No. 1, p. 47.

³ W. Krause, *Die Brechungsindices der durchsichtigen Medien d. menschl. Auges*. Hanover, 1855.

⁴ Helmholtz, *Handbuch der physiologischen Optik*, p. 78.

⁵ Helmholtz, *Op. cit.*, pp. 8-10 and 112-115.

such an extent that the image seen through each is displaced through a distance of one half of its length and that the opposite terminal points of the two images touch (one image appearing to be a prolongation of the other), the length of the image may be calculated from the angle which the two plates make one with the other, providing that the thickness and refractive index of the plates be known. Such an apparatus, so arranged that the angle between the plates may be read off, is termed an 'Ophthalmometer.' In reference to the distance between the refracting surfaces, it may be said that the thickness of the lens (*i.e.* the length of the axis of the lens) may be determined in lenses removed from the eye. Yet it is better, on account of the changes which it undergoes physiologically, to effect this measurement by means of the Ophthalmometer, in the living eye, from the reflected images; the same method is followed in determining the distance between the anterior surface of the cornea and the anterior surface of the crystalline lens.

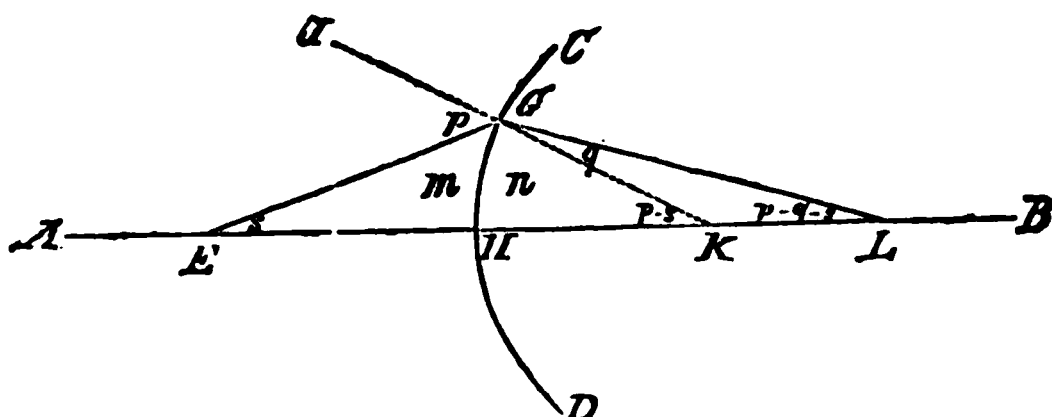
Formation of the Image.

According to the statements which have been made, the eye is a system composed of three *concentric* refracting surfaces. The laws of refraction of such a system may be explained as follows:

1. Let CD (fig. 40) be a spherically curved refracting surface, K the centre of curvature, and AB a straight line which passes through it, *the axis*. Let CD separate two media, of which the one to the left (the *anterior* or first) possesses the refractive index m , the other (the *posterior* or second) the index n .

The luminous ray EG falling from the point E on the axis in the first medium

FIG. 40.



upon the surface CD is refracted at G ; the normal on the surface at the point G is the radius KI , therefore $EGI = p$ is the angle of incidence, $KG L = q$ is the angle of refraction. According to the law of refraction EG , KI , and GL lie in one plane, so that GL must like EG cut the axis. Let the distance, EH , of the point E from the *principal point* H , be equal to a_1 , and the distance of the point L from the principal point H , HL , be equal to a_2 . The relation of the distances a_1 and a_2 is then obtained in the following manner (let the angle $H E G = s$, then the angle $H K G = p - s$, and the angle $H L G = p - q - s$; lastly, let the radius $KH = KG = r$).

According to the law of refraction

$$\sin p : \sin q = n : m \quad . \quad . \quad . \quad . \quad . \quad . \quad (1)$$

In the triangle $E G K$

$$a_1 + r : r = \sin (180^\circ - p) : \sin s \quad . \quad . \quad . \quad . \quad . \quad (2)$$

And in the triangle $G K L$

$$a_2 - r : r = \sin q : \sin (p - q - s) \quad . \quad . \quad . \quad . \quad . \quad (3)$$

If E and H are very distant from one another, or if G and H are very close to one another, then the ray EG is only slightly bent from the direction of the axis; and if it falls upon the refracting surface near the axis, the angles p , q , and s

Thus all rays which are in the first instance parallel to the axis unite after refraction at a point F_2 (fig. 40A) which may be termed the *posterior or second focal point*, and the distance of which from the principal point H $HF_2 = f_2$ (equation 8) is termed the *second focal distance*. Similarly, all those rays which are parallel to the axis in the second medium, unite to form the *first or anterior focal point* F_1 , the distance of which from the centre of curvature, H $HF_1 = f_1$ (equation 9), is termed the *first focal distance*. (Conversely all rays which proceed from the focal points, become parallel after refraction.)

6. From (8) and (9) it follows further that

$$\begin{aligned} f_1 : f_2 &= m : n & . & . & . & . & . & (10) \\ f_2 - f_1 &= r & . & . & . & . & . & (11) \end{aligned}$$

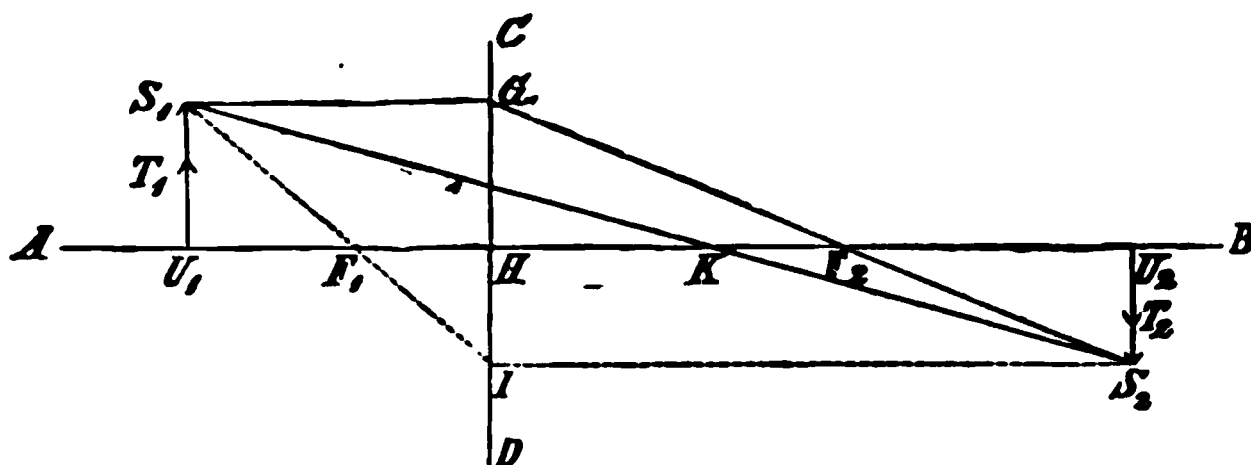
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i.e. the first and the second focal distances are related to one another as the indices of refraction of the first and second media, and the difference between these focal distances is equal to the *radius of curvature* ; thus in fig. 40A, $HF_1 = KF_2$, i.e. the distance of the first or anterior focal point from the principal point H is equal to the distance of the second focal point from the nodal point.

7. The focal points can very usefully be employed in order to find geometrically the image s_2 , which corresponds to a luminous point s_1 .

In fig. 41, let H again be the principal point, K the nodal point, F_1 and F_2 the two focal points. The point of intersection of any two refracted rays proceeding from s_1 must be the point of intersection of all other rays. In order to find this point of intersection we may best make use of the following rays: 1. The

FIG. 41.



unrefracted principal ray, $s_1 K s_2$; 2. The ray, $s_1 G$, which pursues a course parallel to the axis, and passes after refraction through the second focal point, viz. which pursues the course $G F_2 s_2$; 3. The ray $s_2 F_1 I$, which passes through the first (or anterior) focal point, and which after refraction is parallel to the axis, pursuing the line $I s_2$. Any two of these rays suffice in order to find s_2 , and it is easy to prove geometrically that they all pass through s_2 .

By the same construction we can further find that any luminous point T , situated in the line $s_1 u_1$ perpendicular to the axis, will throw its image on the perpendicular $s_2 u_2$ at the point T_2 . All points lying in a plane perpendicular to the axis therefore form images on a plane which is also perpendicular to the axis. Every flat object which is perpendicular to the axis furnishes therefore a flat image perpendicular to the axis, which really, as can readily be proved by geometrical methods, resembles the object.

From § 6 it follows that all luminous points situated at an infinite distance (from the refracting surface) throw their image on a plane which is perpendicular to the axis at the focal point; this plane is termed the *focal plane*. Rays which are parallel to one another, therefore, always intersect at one point of the focal plane.

8. From the preceding there results a simple method of constructing the course of the refracted ray GI , which corresponds to the incident ray EG (fig. 42). Let OP be the focal plane. A ray parallel to EG must intersect the required (refracted) ray at some point (M) situated in the focal plane.

posterior plane. If now in the construction we select two rays which obey also the condition of passing through the foci, they are *ipso facto* perfectly determined. It is naturally most convenient for the purpose of these constructions to select those conjugate planes, the images in which are not merely similar, but of equal magnitude, and which are called *principal planes*.

Their situation is found when in equations (15) and (16) $l_1 = l_2$. It follows then that $a_1 = 0$ and $a_2 = 0$, i.e. the two *principal planes* coincide not only with one another but also with the refracting surface.

12. In the case of two spherically curved refracting surfaces, a straight line which joins their *centres of curvature* constitutes their common axis. As a homocentric pencil of rays falling upon the first surface (providing that its rays do not form too great an angle with the axis) continues homocentric even after refraction, and therefore falls homocentrically upon the second surface, it follows that even after issuing from the second surface the rays are homocentric.

13. Let the distance of the two refracting surfaces along the axis be e ; further let f_1, f_2 be the focal distances of the first, and g_1, g_2 those of the second surface. Let now a_1 be the distance of an object from the first surface, then the first surface casts an image at distance a_2 behind itself.

If this image be situated at the distance b_1 in front of the second refracting surface, then the image cast by this is situated at a distance b_2 behind. The following relations are found to exist:

$$\text{from (16)} \quad \frac{f_1}{a_1} + \frac{f_2}{a_2} = 1$$

$$\text{from (16)} \quad \frac{g_1}{b_1} + \frac{g_2}{b_2} = 1$$

$$\text{lastly} \quad a_2 + b_1 = e.$$

$$\text{Hence} \quad b_2 = \frac{(a_1 e - f_1 e - f_2 a_1) g_2}{(e - f_2 - g_1) a_1 - (e - g_1) f_1} \quad \dots \dots \dots (17)$$

14. Further, if l be the size of the object, l_2 that of its image after passing through the first refracting surface, m_2 the ultimate image after refracting by the second surface, it follows from

$$(14) \text{ that} \quad l_2 = \frac{f_1}{f_1 - a_1} \cdot l_1$$

$$\text{from (15) that} \quad m_2 = \frac{g_2 - b_2}{g_2} \cdot l_2$$

If for b_2 we substitute the value found by (17) we obtain:

$$m_2 = \frac{f_1 g_1 l_1}{(e - f_2 - g_1) a_1 - (e - g_1) f_1} \quad \dots \dots \dots (18)$$

15. If it be required to find the positions of the *principal plane* (§ 11), we must in (18) make $m_2 = l_1$; the distance of the first principal plane from the first refracting surface is then found by the following equation:

$$a_1 = \frac{f_1 e}{e - f_2 - g_1} \quad \dots \dots \dots (19)$$

The distance of the second principal plane from the second refracting surface is found by substituting the value found by equation (19) for a_1 in equation (17):

$$b_2 = \frac{g_2 e}{e - f_2 - g_1} \quad \dots \dots \dots (20)$$

The two principal planes do not therefore coincide, but are separated from one another by

$$a_1 + b_2 + e.$$

16. The ultimate focal point of the rays which before passing through the

fore it must pursue the path D_2s_2 , and s_2 must therefore be the image sought for, which corresponds to s_1 .

19. If now the lengths $H_1U_1 = \Delta_1$ and $H_2U_2 = \Delta_2$, i.e. if the conjugate focal distances be calculated from the principal points, we obtain from an examination of the similar triangles in fig. 43, eq. (16), corresponding to an equation

$$\Delta_1 F_2 + \Delta_2 F_1 = \Delta_1 \Delta_2 \dots \dots \dots (27)$$

If in this equation $A_2 = -A_1$, we obtain

$$\mathbf{A}_1 = \mathbf{F}_2 - \mathbf{F}_1 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (28)$$

which is the distance of that point from the first principal plane, the image of which lies just as far behind the second principal plane.

We have now two new conjugate foci, the two *nodal points* (κ_1 and κ_2 in fig. 43), which are distant from one another to the extent of the difference of both principal focal distances from the principal points. (In the case of a simple refractive surface, there is but a single nodal point, § 2.) As the two nodal points are conjugate points, each ray, which after the first refraction is directed towards κ_1 , *e.g.* $s_1\kappa_1$, *i.e.* each so-called *principal ray*, must after the second refraction pass through κ_2 , and must be parallel to $s_2\kappa_1$, therefore fall on g_2s_2 , because it has yet to satisfy the other condition, *i.e.* to cut the second principal plane at the point g_2 , which corresponds to g_1 (see § 18). It may be easily seen that, in the construction of the image of s_1 , instead of one of the two rays s_1c_1 or s_1d_1 , the ray $s_1\kappa_1$ might also be employed. (The two nodal points are hence axial points possessed of the following characters: each ray which before refraction is directed to the first point, passes after refraction through the second, in a direction parallel to that of incidence. From this property, the position of the nodal points may be directly determined.)

20. If to the previously considered system, composed of two refracting surfaces, we add yet a third refracting surface, or a second system composed of two refracting surfaces, the same simplification may as before be admitted, *as long as all the refracting surfaces have a common axis* (are concentric), i.e. as long as their centres of curvature lie in the same straight line (which could naturally only be constantly the case with two surfaces); for only under these circumstances will a homocentric bundle of rays, falling upon each succeeding surface, make so small an angle with the axis as to continue homocentric. It is always possible then to give, in the case of the whole system, the situation of the *cardinal points*, which serve in the construction of the image, and which are, viz., the two *principal points*, the two *focal points*, and the two *nodal points*.

If the focal distances of two systems have been found, and the distance of their principal planes known, the cardinal points of the resulting system can always be found by means of equations 19-24 and 28.

In order to find the cardinal points for the compound system of the eye, the focal distances of each single refracting surface must be ascertained. Equations (8) and (9) or (8) and (11) are employed with this object.

1. Anterior surface of the cornea: $r=8^{\text{mm}}$, $m=1$, $n=\frac{103}{17}$.

Therefore $f_1 = 23.692^{\text{mm}}$, $f_2 = 31.692$.

2. Anterior surface of the lens: $r=10$, $m = \frac{103}{77}$, $n = \frac{16}{11}$.

Therefore $f_1 = 114.444, f_2 = 124.444$.

3. Posterior surface of the lens: $r = -6$, $m = \frac{16}{11}$, $n = \frac{103}{77}$.

Therefore $f_1 = 74.667, f_2 = 68.667$.

If 2 and 3 be now combined so as to form one (optical) system, *i.e.* if the cardinal points of the lens surrounded by the fluids of the eye be wanted, $e = 4^{\text{mm}}$, $f_1 = 114.44$, $f_2 = 124.44$, $g_1 = 74.667$, $g_2 = 68.667$. Therefore

the first principal point of the lens is situated behind the anterior surface of the lens (according to 19) by about $-a_1 = 2.346^{\text{mm}}$;

the second principal point of the lens is situated in front of the posterior surface of the lens (according to 20) about $-b_2 = 1.408^{\text{mm}}$;

the two focal distances of the lens, which according to 26, in consequence of the indices of refraction of the aqueous and vitreous humour being equal, are equal, are (according to 23 or 24) $F_1 = F_2 = 43.797^{\text{mm}}$.

If now, finally, the cornea is combined with the lens as in the complete system of the eye, we have in this combination:

$$f_1 = 23.692, f_2 = 31.692, g_1 = 43.797, \\ g_2 = 43.797, e = 4 + 2.346 = 6.346^{\text{mm}}.$$

In the case of the eye as a whole

the first principal point is situated (according to 19) at $-a_1 = 2.174^{\text{mm}}$ behind the convexity of the cornea;

the second principal point is situated (according to 20) at $-b_2 = 4.020^{\text{mm}}$ in front of the second principal point of the lens, therefore $4.020 + 1.408 = 5.428^{\text{mm}}$ in front of the posterior surface of the lens, or 2.572^{mm} behind the convexity of the cornea;

the two principal points are therefore distant from one another by 0.398^{mm} .

The first principal focal distance is (by 23) $F_1 = 15.007^{\text{mm}}$, the first focal point is situated therefore 12.833^{mm} in front of the convexity of the cornea;

the second principal focal distance is (by 24) $F_2 = 20.074^{\text{mm}}$, the second focal point is situated therefore 22.646^{mm} behind the convexity of the cornea.

As the distance of the nodal points from the principal points $= F_2 - F_1 = 5.067$

the first nodal point is situated 7.241^{mm} behind the convexity of the cornea, and

the second nodal point is situated 7.639^{mm} behind the convexity of the cornea.

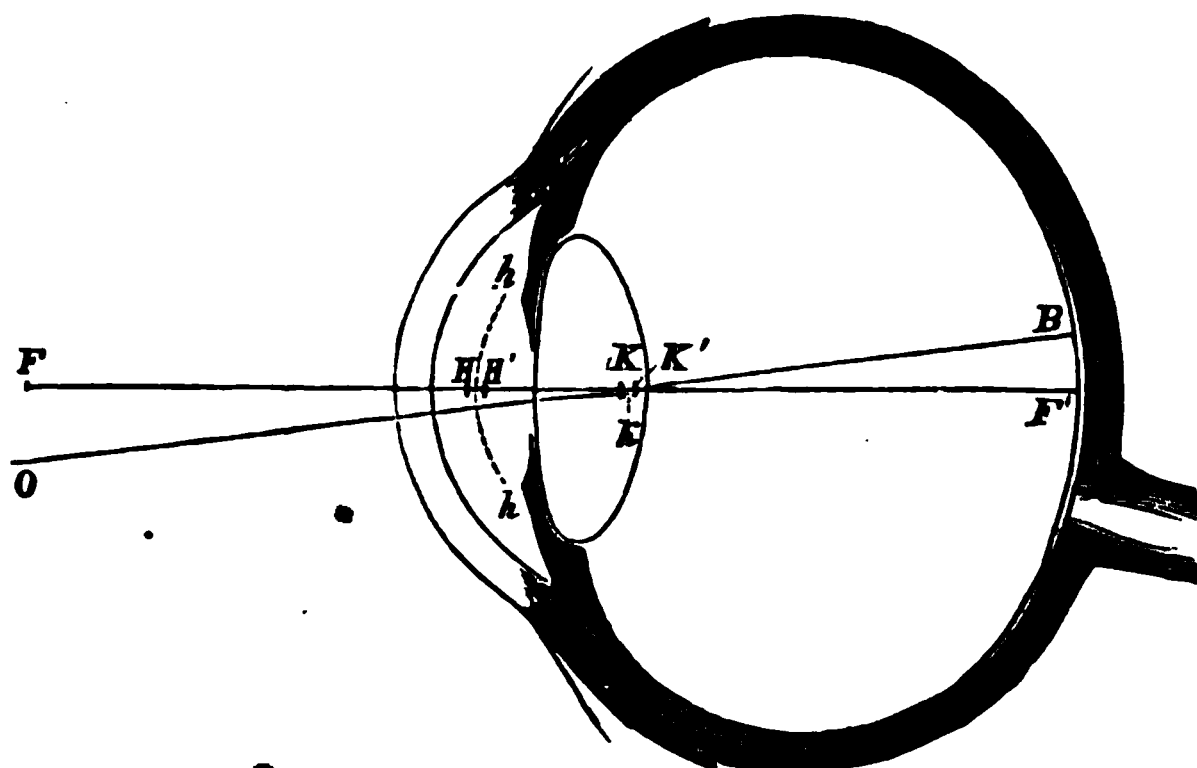
The two principal points are therefore 0.398^{mm} from one

another, about the middle of the anterior chamber of the eye; the two nodal points lie similarly 0.398^{mm} from one another, in the posterior part of the lens, the second focal point being either close to or in the retina.

Fig. 44 exhibits the schematic eye with its cardinal points.

The distance between the two nodal points is so small that in drawings intended for purposes of demonstration they may, without introducing any great error, be united at κ ; similarly, the principal rays may be simply represented by straight lines. (Likewise the two principal planes may be imagined united in the spherical surface hh , which therefore represents the refracting surface of the eye.) If we suppose that all points in the image lie on the retina (on this subject refer to what is said on *Accommodation*), we can for every point in the object easily find the

FIG. 44.



corresponding point in the image, by drawing from the former a straight line passing through the nodal point and falling upon the retina.

Such straight lines (e.g. OB in fig. 44) are called *lines of direction* or visual rays, and the combined nodal points (κ) are included under the terms *point of intersection of lines of direction*; the angle which two visual rays make with one another is called the *visual angle*. If it be desired to ascertain the direction in which lies the point of an object which corresponds to any point in an image, it is only necessary to draw a straight line (*a visual ray*) from the point on the image through the combined nodal points, and to prolong it outwards.

Appendix on the Action of Lenses.

In the case of a lens which is bounded on both sides by atmospheric air, the two principal focal distances are (according to equation 26) equal: by (28), in consequence of this, the nodal points coincide with the principal points.

lens; the distance of the former from the latter, a_1 , is, however, to be considered as negative.

The action of the lens thus interposed is as follows:—

I. When the interposed lenses are convex (f is positive). For every negative value of a_1 , a_2 becomes positive, $a_2 < -a_1$, l_2 has the same sign as, but is less than l_1 , i.e. the interposed convex lens furnishes a real inverted image, but brings it closer to the first lens and diminishes its size. The collecting lens of the compound microscope exerts this action.

II. When the interposed lenses are concave (f is negative).

1. a_2 is positive when $-a_1 < f$, and negative when $-a_1 > f$.

2. l_2 has the opposite sign to l_1 when $-a_1 < f$, and the same sign when $-a_1 > f$.

3. $l_2 < l_1$ when $-a_1 > 2f$; $l_2 = l_1$ when $-a_1 = 2f$; $l_2 > l_1$, when $-a_1 < 2f$.

When a concave lens is interposed between a convex lens and a *real* image, the latter continues to be *real* and *inverted*, providing that the lens is situated at a distance from the image less than its focal distance; on the contrary, the image becomes virtual and erect if the concave lens is more than its focal distance from the image formed by the first lens; the eye-piece lens of opera-glasses has this property. It does not alter the size of the image, if it be at a distance from the object equal to twice its focal length.

On the Images formed on the Retina when the Eye is passive.

When luminous rays proceeding from any object fall into the eye, a definite point in the image corresponds to every point in the object. All the points of the image together furnish an image which corresponds to the object; the image is, naturally, an inverted one. In order to be distinctly perceived, this image must fall exactly upon the surface of the retina. It is evident that for any given eye remaining perfectly passive, there can be only a single surface, the image of which can fall exactly on the retina. The form and the distance of this surface may be determined from the optical values of the eye. Each point of the object which does not lie in this surface has its corresponding point in the image lying, not in the retina, but in a plane before or behind it. In both cases the retina cuts the pencil of refracted rays proceeding from the object, in the first case after, in the second before, they have united to form points in the image; in both cases, instead of a luminous point being formed on the retina, there 'is a circle of diffused light,' i.e. a small circular area is lighted up: this corresponds to a section through the luminous cone.

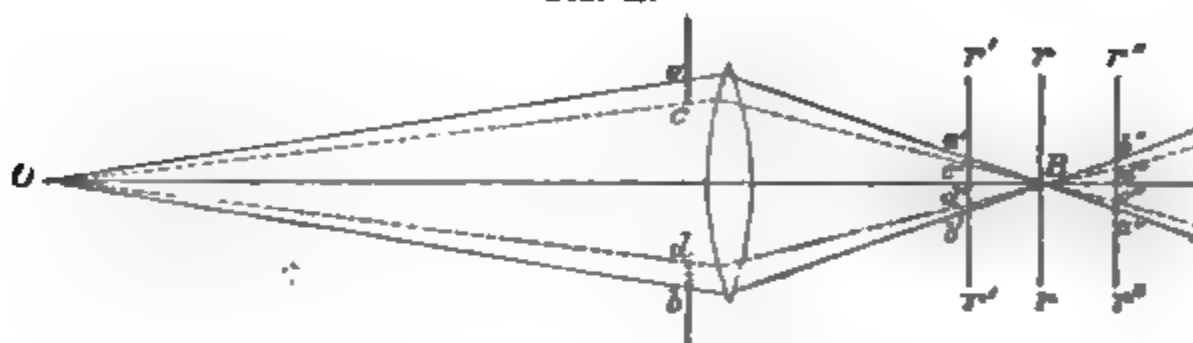
In fig. 45, B represents the point of the image of the object o , which falls upon the retina rr . If, however, the retina lies in front of the point in the image (*viz.* at $r' r'$), or behind it (*e.g.* at $r'' r''$), circles of diffused light are formed, which have the diameters at $a' b'$ or $a'' b''$.

Hence it follows that, strictly, an immovable eye can only distinctly see objects lying in one plane, and at a perfectly definite distance. All objects or portions of objects which lie outside

the plane, furnish indistinct, blurred, images, in which *circles of diffusion* instead of points correspond to the luminous points of the object.

The size of the circle of diffusion depends, *ceteris paribus*, upon the dimension of the cone of luminous rays which reaches the eye, and this again depends upon the width of the pupil, the inner border of which limits the luminous cone. If, therefore, the pupil contracts, or if it be replaced by a small aperture placed in front of the eye, as *e.g.* by a hole made in a card, then the circles of

FIG. 45.

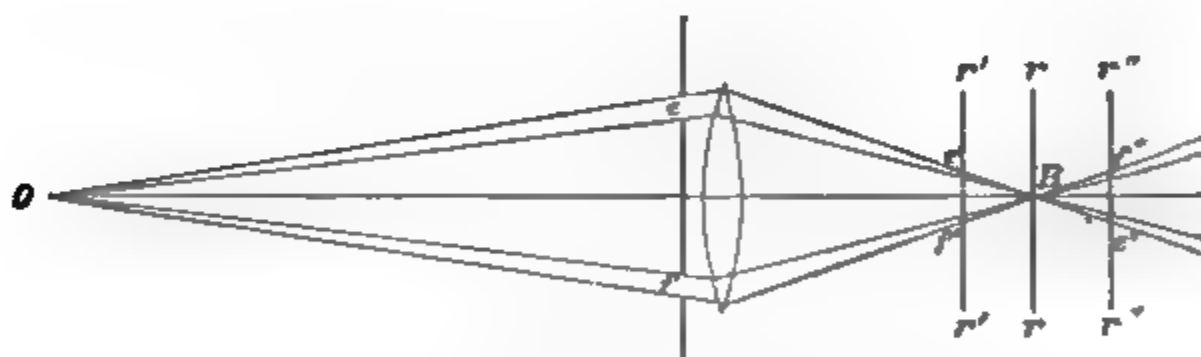


diffused light will, *ceteris paribus*, become smaller, and consequently the image will be sharper. In fig. 45, if *cd* represents the aperture of the contracted pupil, it can be easily seen how the contraction diminishes the diameters of the circles of diffusion to *c'd'* and *c''d''* respectively.

If the pupil be replaced by two small openings, if, *e.g.*, a card which has been perforated in two places by a pin, be placed in front of the eye, the distance between the perforations being smaller than the diameter of the pupil, two smaller luminous cones are as it were cut out of the larger one, and instead of one 'circle of diffusion' being formed upon the retina, there are two smaller.

In fig. 46, let *e* and *f* be the holes in the card which replace the pupil; the

FIG. 46.



two luminous cones reunite at B; the retina, if it is not situated in the plane *rr*, but in two planes, *r'r'* or *r''r''*, receives, instead of the luminous point B, two circles of diffused light, *e'f'* and *e''f''* or *e'f'* and *f''f''* respectively.

All objects which are so placed in reference to the eye, as to throw a diffused image upon the retina, would in the case just considered throw two diffused images, and therefore be seen double (Scheiner's experiment).

Accommodation.

Daily experience, however, teaches us that a normal eye is capable of seeing objects distinctly which are placed at almost any distance; there must therefore exist an arrangement capable of

altering the eye, and dependent upon the will. The changes in the eye which occur as a result of this arrangement are included under the term *accommodation*. It is not known with certainty for what distance the eye is adjusted when it is not actively accommodated. It was formerly supposed that the eye when at rest was accommodated for a medium distance, and accommodation was therefore supposed to occur in two directions, in one direction for near objects (positive accommodation), and in another for distant objects (negative accommodation). Now, however, it is almost universally supposed that the normal eye when at rest is adjusted for infinite distances, *i.e.* that the focal point of the normal passive eye lies on the retina. It follows from this that accommodation only occurs in one direction, *i.e.* for near objects.

The principal grounds upon which this view is based are: 1. When the eyelids which have been long closed are suddenly opened, the eye is found to be adjusted for distant objects (Volkmann). 2. The vision of distant objects, unlike the vision of near objects, is not accompanied by a feeling of exertion. 3. Atropia, which paralyzes the apparatus concerned in accommodation, causes an unchangeable adjustment for objects which are as distant as possible from the eye; if a negative apparatus for accommodation did exist, one would have to make the improbable assumption that under these circumstances it was thrown into a state of tetanic activity at the same time that paralysis of positive accommodation occurred (Donders). 4. Even in cases of neurotic paralysis of the apparatus of accommodation (as when the third nerve is paralysed) the eye is always accommodated for infinite distance, whilst no paralytic condition is known in which the eye is accommodated for near objects.

Accommodation might depend upon the following changes occurring in the eye. 1. Changes in the indices of refraction of the media of the eye. 2. Displacement of the surface of projection (retina), analogous to the artificial accommodation in the *camera obscura*. 3. Alterations in the forms of the refracting surfaces. It is self-evident that the first changes do not occur. A displacement of the retina in the direction of the optic axis would be possible by a lateral compression of the eyeball brought about by the *recti* muscles of the eye; this influence, which was formerly assumed in order to explain accommodation, must be unimportant, seeing that even in eyes which have been cut out of the body changes of accommodation can be occasioned. Changes in the *form* of the refracting surfaces must, therefore, be possible. These have actually been discovered, and they have been found to occur in the crystalline lens.

When the eye is accommodated for near objects, the anterior surface of the lens becomes more strongly curved, and approaches closer to the cornea; this is especially the case with that portion which is not covered by the iris, and which arches forwards through the pupil (Cramer).

These changes are proved by the following experiment:—

If a lighted candle be placed at one side of the eye, and if one looks into the eye from the other side, three distinct little images of the flame are seen, which are due to reflexion from the refracting surfaces of the eye: the first, erect (virtual), is formed by the anterior surface of the cornea; the second, which is also erect, but much weaker, is formed by the anterior surface of the lens; the third is brilliant, inverted (real), and is formed by the posterior surface of the lens. If the eye now looks fixedly at an object close to it, the second image becomes perceptibly smaller, and approaches somewhat the first image, affording a proof that the anterior surface of the lens becomes more strongly convex and moves forwards.

Changes of an opposite character occur when the eye stares into infinite distance (Purkinje and Sanson's experiment, Oramer). Instead of a flame, it is more convenient to apply one or two luminous points (holes in a screen); the distance between the reflected images of these points can then more easily be measured by means of the ophthalmometer than the size of the image of a flame (Helmholtz).

The protrusion of the iris, which is brought about by an increase in the curvature of the anterior surface of the lens, may be shown in the following way: the caustic line (due to refraction through the corneal surface), which shows itself upon the opposite half of the iris when the eye is lighted from the side, changes when the eye is accommodated for near objects then approaching the margin (Helmholtz).

The following table (Helmholtz) exhibits the changes in the optical constants of the eye which occur during accommodation; the places are calculated from the convexity of the cornea, and are reckoned from behind as positive, from the front as negative. The numbers for the condition of rest have been given at pages 376 and 384, slightly modified from those given by Listing for the typical eye.

	Eye at rest : adjusted for distant view	Eye accommo- dated : adjusted for near view
Radius of curvature of the cornea . . .	8	8
" " anterior surface of the lens }	10	6
" " posterior surface of the lens }	6	5.5
Position of anterior surface of the lens . . .	3.6	3.2
" posterior " " . . .	7.2	7.2
" first principal point	1.9403	2.0390
" second " "	2.3563	2.4919
" first nodal " "	6.957	6.515
" second " "	7.373	6.974
" first focal " "	-12.918	-11.241
" second " "	22.231	20.248
First focal distance	14.858	13.274
Second " "	19.875	17.756

Accommodation is chiefly effected by the ciliary muscle (M. ciliaris, M. tensor choroideæ, Brücke's muscle). This muscle is composed of both radiating and circular fibres. The first, which constitute the chief part of the muscle, arise from the point of reflexion of the membrane of Descemet, where it passes from the

cornea to the iris (lig. iridis pectinatum), and are inserted into the ciliary processes of the choroid; the unimportant circular fibres, which are situated on the inner side of the radiating fibres in the most anterior part of these muscles, surround the border of the crystalline lens. The radiating fibres pull forwards the anterior border of the choroid coat, and so draw the choroid and the retina together like a bag, around the vitreous body (whereby the latter presses the lens forwards). The *zonule* of *Zinn*, the tension of which during the state of rest draws the border of the lens backwards and outwards, and thus flattens the lens, becomes relaxed owing to its posterior insertion being approximated to its anterior (the border of the lens), and thus causes the lens to become thicker (less flat). (Helmholtz.)

The circular fibres appear to co-operate by drawing the ciliary processes inwards, and thus leading to a relaxation of the zonule of Zinn (F. E. Schulze).

The iris also takes a part in the accommodation of the eye for near vision. On the one hand, the part which it plays is passive, in that it assumes a more arched form merely as a result of the greater convexity of the anterior surface of the lens, for the border of the pupil lies immediately in contact with the capsule of the lens;¹ on the other hand, it plays an active part, by the contraction of the pupils. (For the movements of the iris see below.) The contraction of the pupil does not appear to be indispensable to accommodation, seeing that the latter is possible when the iris is wanting or imperfect. Its significance in accommodation is probably to be sought for in the fact that when a lens becomes more convex its spherical aberration increases, and consequently a greater number of the marginal rays require to be screened off. The independence of contraction of the pupil and accommodation is also proved by the fact that the latter precedes the former (Donders).

The nerve fibres which are concerned in accommodation are contained in the ciliary nerves; when these are irritated the eye is accommodated for near vision (Völckers and Hensen). It is in the highest degree probable that these fibres are derived from the third nerve (motor oculi).

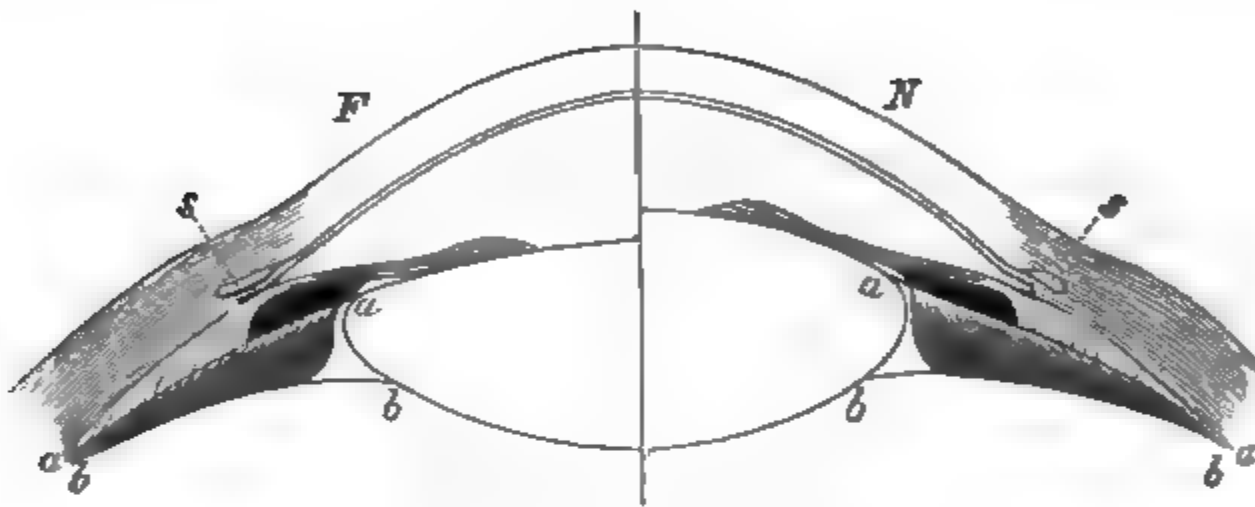
Fig. 47 exhibits a section of the anterior segment of the eye; on the left-hand side the line is shown adjusted for distant vision, on the right for near vision (after Helmholtz).

Concordant data are yet wanting concerning the rate at which the act of accommodation proceeds; the rate is, however, tolerably slow. The change from the state of activity to that of rest occurs more rapidly than the reverse (Hensen and Völckers).

¹ The proof of this statement is afforded by the fact that no shadow of the iris falls upon the lens (Helmholtz); nevertheless only the margins of the iris are in contact with the lens, for between the other parts of the iris and the lens there exists a posterior chamber filled with fluid (Hensen and Völckers).

There appears to exist a yet imperfectly investigated central connexion between the nerves which are concerned in accommodation, and those which supply the iris and the external muscles of the eyeball. In favour of such a connexion the following facts may be cited:—1. The behaviour of the pupil in accommodation (see above). 2. Rotation of the eyeball inwards is associated with contraction of the pupil and involuntary accommodation for near vision (Czermak). 3. Atropia, which dilates the pupil, paralyzes at the same time, as has been already stated, the accommodating mechanism; conversely Calabar bean occasions contraction of the pupil and tetanic accommodation for near view.

FIG. 47.



s s, canal of Schlemm; *a a b b*, the folds of the zonule of Zinn, which are intercalated between the ciliary processes; the latter are partly hidden and covered by the former (the section is so arranged that a fold of the zonule lies in front of the ciliary process). The radiating fibres of the ciliary muscle are seen springing from *s*.

According to some writers, the movements of accommodation always follow a parallel course in the two eyes; others dispute this statement.

For every eye there are definite limits of clear vision; the furthest point, the image of which can fall exactly upon the retina, is called the '*far-point*' (*punctum remotum*); the nearest point is called the '*near-point*'; the distance between them is called the *region of distinct vision*. In the case of normal eyes the '*far-point*' is infinitely distant; the '*near-point*,' which is nearer the eye the more active the apparatus of accommodation, is at a distance of between 0·2 to 0·3 metre from the eye.

In many eyes which are otherwise normal, the focus during rest does not, as usual (in the *Emmetropic* eye), fall upon the retina, but in consequence of an abnormal length or shortness of the optic axis, it either falls in front of the retina (*Myopia*) or behind it (*Hypermetropia*). The *distant point* of myopic eyes therefore lies abnormally near, the distant point of hypermetropic eyes, on the contrary, is more than infinitely distant—i.e. in order to perceive objects which are at an infinite distance the hypermetropic eye must perform movements of accommodation. The activity of the accommodating mechanism being the same, the near point of the myopic eye must be abnormally near, that of

the hypermetropic eye must be abnormally distant. Hence myopic eyes are 'short-sighted,' and hypermetropic eyes 'long-sighted.' Other abnormalities depend upon a small degree of activity of the accommodating mechanism; these naturally only exert an influence upon the situation of the point of near sight, not upon that of distant vision.

The defective or excessive refraction of abnormal eyes—i.e. the relatively too great or too small curvature of their lens, can be corrected by glasses (spectacles); these must naturally, in the first case (in Myopia), be concave; in the second (in Hypermetropia) be convex.

Even deficiency in the power of accommodation may be corrected by artificial accommodation, by means of the temporary use of spectacles. The simplest method of determining the situation of the near and distant point is by ascertaining at what distances the eye can readily recognise distinctly an object which is brought near to or which is removed from it, as, e.g. at what distance letters can be read. This method is, nevertheless, inexact, because the diminution of the *visual* angle by distance makes the object less easily recognisable. A much better method consists in determining at what distance an object throws a clear, and at what distance a diffused, image on the retina. For this purpose Scheiner's experiment (p. 388) affords the best means of investigation. If an object (e.g. a pin's head) be looked at through two holes in a card placed close to one another, it appears single if the eye be accurately adjusted, but under opposite circumstances it appears double. If the object be brought closer to the eye, or, on the contrary, removed from it, the space in which it is clearly seen is the field of distinct vision. On this property are based various apparatuses which are used in selecting spectacle-glasses—so-called '*optometers*.' In the best-known optometer (Stampfer's) the object is an illuminated slit, the distance of which from the eye can be altered and measured at the same time. As age increases, even after the fifteenth year (MacGillavry), the capability of accommodating for near objects diminishes, presumably in consequence of an induration of the lens (Donders).

Iris and Pupil.

The iris with its central aperture, the pupil, serves at once as a diaphragm to shut off the marginal rays (being thus analogous to the *diaphragms* of optical instruments), as well as to regulate the amount of light entering the eye, and as an auxiliary to accommodation. The size of the pupil depends upon the state of contraction of the two antagonistic sets of muscular fibres in the iris, the sphincter and dilator, fibres of the pupil. The first form a circular layer around the pupil, the second have a radiate arrangement; the first derive their nervous supply from the motor oculi, the second from the sympathetic. If both sets of fibres or their nerves are subjected to the same stimulus, the sphincter fibres predominate and the pupil contracts. Usually both nerves are in a certain state of excitation (tonus), for when one is cut through, the muscle governed by the other predominates. If the cervical sympathetic be divided the pupil contracts; if the third nerve be divided it dilates.

Recently the existence of a dilator of the pupil has been denied in mammals (Grünhagen, Hampeln). The older view is supported by nearly all the statements of anatomists (lately Henle, Merkel, Dogiel and v. Hüttenbrenner); by the dilatation of the pupil when the sympathetic is irritated (those who deny the existence of dilating fibres maintain that this dilatation is a vaso-motor effect); and, lastly, by the circumstance that direct excitation of the border of the iris is able to cause local circumscribed dilatation (Bernstein and Dogiel, Engelhardt).

The fibres of the *motor oculi* which cause contraction of the pupil pass to the eye through the *ciliary ganglion*; this is, however, not the case with the fibres of the *sympathetic* which cause dilatation of the pupil. The latter take their origin first of all in the spinal cord, in the neighbourhood of the lower cervical and superior dorsal vertebræ (cilio-spinal centre of Budge). In pathological conditions, when this region is irritated, the pupil dilates. The real centre for these fibres is, however, situated in the higher regions of the cord, presumably in the medulla oblongata (Schiff).

In the head, the fibres which dilate the pupil run in the course of the fifth, the irritation of which occasions dilatation, and the section of which prevents the effect which follows irritation of the sympathetic.

Seeing, however, that after division of the sympathetic the pupil does not contract so powerfully as after the division of the fifth, we must conclude that the fifth contains special fibres capable of dilating the pupil. The origin of these fibres can, in frogs, be traced to the Gasserian ganglion (Oehl, Rosenthal, Hirschmann, S. Guttmann). There exist, however, opposite statements concerning the influence of the fifth pair on the pupil (Rogow).

Movements of the iris occur principally under the following circumstances:

1. *Irritation of the optic nerve occasions contraction of the pupil*, by irritating in a reflex manner the motor oculi. The pupil contracts, therefore, when light falls into the eye, and the more strongly the more powerful the light. In this way the amount of light which reaches the retina is partly regulated. Contraction of the pupil also occurs when the trunk of the optic nerve is irritated (Mayo), and ceases after division of the *motor oculi*. Irritation of one optic nerve is sufficient to cause contraction of both pupils. Generally, under normal circumstances, both pupils are of the same size (Donders).

2. *When the eye is accommodated for near vision the pupil contracts*. Poisons which occasion tetanic accommodation for near vision (Calabar bean) also cause contraction. This contraction is caused by an excitation of the nerves which contract the pupil, and is to be looked upon as a kind of 'associated' movement (Chap. XI.)

The contraction of the pupil which is caused by light commences, on an average, about 0.49 sec. (0.4 Listing) after the irritation, and the maximum effect (contraction) occurs 0.58 sec. after the irritation.

The contraction connected with accommodation begins 0.41 sec., and reaches its maximum 1.13 sec. after the cause which occasions it. The dilatation which

follows irritation of the sympathetic commences in rabbits 0·89 sec., and reaches its maximum 3·40 sec. after the commencement of the irritation (Arlt, jun.)

3. *Rotation of the eyeball inwards occasions a contraction of the pupil*, as a kind of 'associated' movement, by irritation of the motor oculi.

As the eyes are during sleep turned inwards and upwards, the contraction of the pupils which is observed during sleep can be explained.

4. *During dyspnœa the pupils are dilated*; this dilatation ceases when asphyxia sets in. This dilatation depends upon irritation of the centre which exists in the cord and which presides over the pupil, for it does not occur if the sympathetics have been previously divided.

5. *Powerful irritation of sensory nerves causes, in a reflex manner, dilatation of the pupil* (Bernard, Westphal).

6. *Violent muscular efforts* (especially powerful inspiratory and expiratory movements) *are associated with dilatation of the pupil* (Romain-Vigouroux).

In addition, in the normal state, a very slight alteration of the pupil is observed to occur with every beat of the pulse, as well as with every expiration; every flow of blood to the iris appears especially to occasion a contraction of the iris; in this way may be explained the contraction of the pupil which follows withdrawal of the aqueous humour (Hensen and Völckers).

7. Numerous poisons, either when introduced into the blood or topically applied, induce changes in the size of the pupil. Atropia, for example, dilates the pupil by causing a paralysis of the terminations of the third nerve in the circular fibres of the iris. Nicotia, physostigma, morphia, &c., cause contraction of the pupil (*Myosis*). This is due, according to some (Hirschmann, Rosenthal), to a paralysis of the terminations of the sympathetic in the dilating (radiating) fibres, but, according to others (Grünhagen), to irritation of the third nerve. Anæsthetic poisons (chloroform, alcohol, &c.) occasion in the first place a contraction, and afterwards a dilatation of the pupil.

The kind of action which these poisons exert is still matter for controversy. Meanwhile the supposition that they all exert an action upon the sphincter arrangement of the iris appears the most probable, seeing that the poisons under dispute exert a simultaneous and corresponding action on the apparatus engaged in accommodation. It is especially a matter of doubt whether the poisons which induce contraction (*Myotics*) act by paralysing the sympathetic; in support of the latter view it is stated that irritation of the sympathetic does not exert any action upon the pupil of animals under the influence of such poisons; this result might be due to the intensity of the tetanic contraction of the sphincter fibres.

Further, the circumstance that the action of atropia manifests itself even after division of the ciliary ganglion (Hensen and Völckers), and that the action of these poisons occurs when they are dropped into the eye, render it very probable that yet unknown ganglionic centres exist either in the iris itself, or in its immediate proximity (v. Bezold).

When one pupil is dilated by atropia, the other contracts and remains contracted in consequence of the large amount of light which falls into the first eye.

Imperfections of the Retinal Image.

From what has been stated in the preceding pages it is seen that a sharp, diminished, and inverted image of any object brought within the field of distinct vision can be formed on the retina. Yet the absolutely faultless production of such images is rendered impossible in consequence of certain properties of the eye, which it shares with other optical instruments: these are—

1. *Chromatic Aberration.* White light, as is well known, is decomposed by refraction into its coloured components, in consequence of the unequal refrangibility of the latter. Consequently, if white light proceeds from a point in an object, the latter, instead of having a single spot corresponding to it in the image, must have a series of such points lying one behind the other, the most anterior point corresponding to the most refrangible (violet), and the most posterior to the least refrangible (red) rays. The eye cannot therefore be thoroughly accommodated for a white object: if, for instance, it is so accommodated that the image of the violet rays falls upon the retina, the remaining colours appear in concentric diffusion rings, which are larger the further the colour is separated from violet; as, however, all the diffused rings and the violet spot fall on the middle, there results a white spot with coloured borders. Similarly every white object must appear white with coloured borders, as the coloured images are superimposed as far as the margins.

If the eye be accommodated for a colour which lies in the middle of the spectrum, as for green, there result, naturally, two series of coloured diffused images; these cover one another to such an extent to the very borders that the *complementary colours* (see below) fall upon one another, and the borders even appear in great part to be white. The latter circumstance is one cause why in ordinary vision we do not see the coloured borders of the objects which are looked at; these coloured borders, moreover, in consequence of the slight dispersive power of the media of the eye (the dispersive power of which is nearly the same as that of distilled water), are very slight, and disappear entirely when contrasted with the powerful white light which falls upon the middle of the eye; possibly, too, the combination of the different ocular media tends to make the eye achromatic (the arrangement being analogous to the combination of flint and crown-glass lenses in optical instruments). In order clearly to perceive these coloured margins, the eye must be accommodated, not for a colour in the middle of the spectrum, but for a colour at the extreme end (red or violet); this is obviously best done by not accommodating for the object.

White fields appear, when the eye is accommodated for too great a distance, to possess a faint reddish-yellow margin; when the eye is accommodated for too near a distance the margin is blue (Helmholtz); a luminous point seen through a reddish-violet glass appears, when the eye is accommodated for the red rays, to be red with a violet circle of diffusion; in other cases the converse occurs (Helmholtz). From what has been stated it also results that the extent of the field of distinct vision is various for these different colours. Naturally the point of near and distant vision for violet light must be appreciably nearer than for red, a fact which can be proved by looking through a telescope at equally distant spots of various colours, when the glass must be adjusted differently in order that all the colours should be seen with equal distinctness (Fraunhofer).

Red surfaces appear nearer than blue surfaces which are in the same plane, because the eye has to be more strongly accommodated for the former, and therefore judges the object to be nearer (Brücke).

2. *Spherical (monochromatic) Aberration.*—As has been already frequently stated, the rays which proceed from the point in an object can only join again to form the point of an image when they fall upon the spherical refracting surface within a very small distance of the axis. This condition is in part satisfied by the iris when it cuts off a large number of the peripheral rays which fall upon

the eye. A further correction is effected by the form of some of the refracting surfaces of the eye; being *ellipsoids*, their curvature diminishes decidedly near the margins. Moreover, in the case of the lens, the rays which pass through its borders only traverse the outer layers, which possess smaller powers of refraction than the inner. This correction is, however, never perfect, being sometimes not sufficient, sometimes too great, so that nearly always, especially when the pupil is dilated, a certain amount of aberration is present, which gives rise to circles of diffused light, and consequently to indistinct images.

Sometimes a defective centring of the refracting surfaces of the eye can be discovered (Brücke).

Some other forms of monochromatic aberration are the following:—

Astigmatism (Helmholtz, Knapp, Donders).—*a.* So-called ‘irregular astigmatism’ depends upon various deviations in the curvatures of the refracting surfaces, so that the union of a homocentric pencil of rays at one point is hindered; each small segment of the surface has its special image, so that an object such as a point throws a star-like (fixed star) image upon the retina. The cornea, moreover, is subject to transitory inequalities of its surface (tears, &c.) *b.* ‘Regular’ astigmatism depends upon a difference of the curvature of the refracting surfaces in different meridians. The two meridians which are furthest removed from one another are called principal meridians. As a rule, the vertical meridian is more arched than the horizontal. The two meridians, therefore, possess different focal distances, so that the eye may be short-sighted in the vertical meridian, and long-sighted in the horizontal. Generally, however, the difference is so slight that it can only be discovered by looking at fine parallel lines from a distance; these can be seen from a greater distance when vertical than horizontal. When the degree of astigmatism is very great, it is corrected by a glass which is stronger in one direction than the other, or, more simply, which is only curved in one direction, which is, therefore, *cylindrical*.

3. *Fluorescence*.—All the media of the eye are fluorescent; the lens is most so (Helmholtz, Setschenow, Regnaud). As the sensitiveness of the retina is restricted so as to permit of its only appreciating waves of a certain length, the fluorescent property of the media tends to increase the range of perception for light of smallest wave-length (ultra-violet rays). Of the true limits more will be said below.

4. *Polarization*.—If polarized blue light, or light which contains blue, falls on the eye (for example, if we look at the sky through a Nicol’s prism, or even with the naked eye, as the blue rays of the sky are already polarized), a tuft-like image (Haidinger) is seen, which moves with the eye. The powers of double refraction which the ocular media possess (Janin, Valentin) are not sufficient to explain this phenomenon. It appears to depend upon the (presumably doubly refracting) fibres of the yellow spot (see below), which being struck by the polarized light at different angles, absorbs at one place more, at another less, giving rise to the appearance above mentioned (Helmholtz).

On the behaviour of Light which penetrates the Eye.

The luminous rays after penetrating the eye are in part absorbed and in part reflected, so that issuing from the eye they follow the same course which they pursue on entering. Each bundle of homocentric rays entering an eye which is perfectly accommodated is, after refraction, brought to a focus on one point in the transparent retina, presumably on its outer layer (of rods and cones). Each rod¹ is to be looked upon as a prism of very

¹ According to recent researches it is only the external segments of the rods or of the analogous cones which have this function.

high refractive power the base of which touches the choroid, and which at its margin lies in contact with a feebly refracting *intermediate substance* (Brücke). The rays which, after uniting to form points in the image, again diverge, come in part in direct contact with the choroid (axial rays) and in part strike the sides of the rods, but at so oblique an angle, that instead of being refracted by the *intermediate substance*, they undergo *total reflection*. Ultimately all these rays must be thrown upon the choroid. Here they are almost all absorbed by the black pigment; the unabsorbed rays, however, are reflected, in part directly (axial rays), in part after reflection from the sides of the rods. According to well-known optical principles, they ultimately return again to the point in the object from which they emanated. By this arrangement the passage of rays from one part of the retina to the other (phenomena of interference, &c.) is avoided, and clear vision is made possible. Upon this arrangement, too, depends the fact that on looking into the eye the fundus always appears dark.

In order to see the fundus of the eye illuminated, the observer must make his own retina the point of departure of rays which are perceived on their return from the observed eye. This object is attained by the use of the *ophthalmoscope*. By means of this instrument the light of a flame is thrown into the eye as if it came from the eye of the observer.

One of the simplest ophthalmoscopes (Helmholtz's) consists of an arrangement of glass plates, which serves at once as a mirror and as a transparent medium. By means of this arrangement of plates the luminous rays from a light placed at the side of the observed eye are thrown into the latter. The rays which return after reflection from the fundus are only in part thrown back by the plates to the source whence they first emanated (the light); in part they traverse the plates and reach the eye of the observer. The observed eye appears in this way to be diffusely illuminated with a red light.

A clear image of the fundus of the eye may further be obtained in the following manner. When the observed eye is placed at a certain distance, the retina is somewhat behind the focal point of the optical system, which, like the object-glass of a microscope, throws a real, inverted, and enlarged image of the retina in that plane to which the eye is turned. As this image, in consequence of its large size (which only permits of a small part of it falling at once upon the pupil of the observer), and on account of its continually changing position, cannot be observed, an auxiliary lens must be employed: this is either a collecting convex lens, which makes the image smaller, brighter, and brings it nearer to the observer, whilst it allows it easily to be fixed in one place, or it is a concave lens, which possesses similar properties, but which furnishes a distinct and erect image.

The combination of glass plates in the instrument above referred to may be replaced by a plane or concave mirror; which, being furnished with a central aperture, permits a portion of the rays returning from the fundus of the observed to reach the observing eye; upon this plan other ophthalmoscopes have been constructed (those of von Ruete and Coccius). Between the source of light and the (plane) mirror, a convex lens may be placed with the view of concentrating the rays. If it be desired merely to see the eye diffusely lighted up, and not to obtain a sharp image of the retina, the following procedure may be had recourse to (Brücke). The eye which is to be observed is fixed upon a near luminous object, but is accommodated for distant vision. Instead of the rays of light then converging to points, circles of diffused light are formed upon the retina. The reflected rays which leave the eye under these circumstances do not again meet at the points whence they emanated, but either far behind them or they do not meet at all (i.e. they are either parallel or divergent). If now the observer's eye is placed in the path of the cone of the returning rays (being protected, if needs be, from the direct influence of the flame by a screen), the observed eye is seen to be illuminated, of a red tint.

The eyes of human and animal albinos exhibit, without any special arrangement being required, an illuminated fundus, as light passes through the sclerotic and choroid, and falls into the eye. The illumination of the eye is especially brilliant in animals, in which over a portion of the choroid the black pigment is replaced by a bright, shining, strongly reflecting membrane, the so-called *tapetum* (this is seen in the eyes of many of the *mammals*, especially in beasts of prey, and cetacea, in fishes, &c.)

Vision.

The rays which fall upon the retina lead to the perception of light, in consequence of the vibrations of the ether affecting in an unknown manner the terminations of the optic nerve in the retina.

The only nerve terminations which are to be considered sensitive to light are *the rods* and *the cones* (H. Müller). The proofs for this statement are the following:—

1. The point of entrance of the optic nerve, where the retina consists of nerve fibres without either rods or cones, is insensitive to light; this is therefore called *the blind spot* (also Mariotte's spot). If we look fixedly with the right eye at the spot A (keep-

A
●

B
●

ing the left eye closed), holding the paper at a distance from our eye four times as great as the distance of A from B, the point B will not be seen. In this case, by looking at A, its image falls upon the termination of the optic axis, and the image of B falls upon the point of entrance of the optic nerve, which is situated about $3\frac{1}{2}$ mm on the inner side. Likewise A disappears, if B be looked at fixedly with the left eye at the same distance as in the previous experiment. The function of the blind spot in the field of vision will be discussed below.

2. The *fovea centralis retinae* and the *macula lutea* which surrounds it, which contain rods and cones, but no fibres of the optic nerve, are fitted for the most acute vision (the fovea centralis

almost exactly coincides with the termination of the optic axis); the image of any fixed object which is looked at falls upon this part of the retina. As the fovea centralis only contains cones, and the macula lutea cones in large numbers (one cone being surrounded by a circle of rods), and as the remaining part of the retina contains only few cones (one cone surrounded by many circles of rods), we are entitled to conclude that the cones are even more sensitive to light than the rods.

3. When the eye is illuminated from without, the vessels of the retina which are situated behind the layer of fibres, but anterior to the layer of rods and cones, cast a shadow; as this shadow can be perceived *entoptically*, under certain circumstances which will have to be discussed (Purkinje's figures), it is proved that the rods and cones are the structures which are sensitive to light. By accurate measurement it has been determined that the shadows which are perceived really are shadows of the blood-vessels of the retina, and not of other vessels situated in front. For example, by moving the source of light, the position of the shadow changes, and as these changes of position can be measured entoptically, the distance of the bodies which cast the shadows from the sensitive surface can easily be calculated. The distance agrees exactly with the distance between the vessels of the retina and the rods, as ascertained by direct measurement (H. Müller).

The end-organs, the rods and the cones, are, therefore, the only organs which are directly capable of being excited by the vibrations of the ether; this property not being shared by the fibres of the optic nerve either in the retina or in the trunk of the nerve. Irritation of the optic nerve, at any point in its course or terminations, by any of the usual nerve excitants (mechanical, electrical, &c.) gives rise to the sensation of light, which, therefore, constitutes the 'specific energy' of the optic nerve.

In the living eye the retina possesses a purple-red colour, and this colouration which is the cause of the red colour of the illuminated *fundus* is situated in the external segments of the *rods*; light bleaches this colour rapidly; during life, however, the colouring matter is continually being regenerated (Boll).

The investigation of the relations which this colouration bears to the excitation of the retina has but recently been commenced (Boll, Kühne) (1).

Mechanical irritation, as contusion or section of the trunk of the optic nerve, leads to a lightning-like illumination of the whole field of vision. Pressure applied to the eye or to a limited part of the retina leads to circular bright 'pressure-figures,' 'phosphenes,' upon the corresponding (opposite) side of the field of view; in eyes which are morbidly excitable, the contact of the circulating blood with the retina is sufficient to occasion manifestations of light (sparks, images of the vessels); lastly, a sudden change in the accommodation of the eye in the dark, by causing a traction upon the anterior margin of the retina, gives rise to the appearance of a bright fringe at the border of the field

of view (Purkinje, Czermak). Electrical irritation (passage of a constant current through the eye, or variations in the intensity of the current) also occasions peculiar appearances of light, different parts of the retina being perceived (Ritter, Purkinje). For the influence of electrical irritation upon the perception of colour, see below.

In order to bring about an excitation of the retina the luminous impression need only act upon it for a very short period (the time of duration of an electric spark suffices). When light continues to act upon the retina for a long time, the excitation becoming more intense, fatigue of the retina results. These facts explain the following: 1. The appearance of *negative* 'after-images' (see below). 2. The much greater sensitiveness of the retina after the eye has been in darkness for considerable periods. 3. The greater effect produced by intermittent luminous stimulations as compared with those which are continuous. The effect of such intermittent stimulations is most marked when they follow one another seventeen or eighteen times in each second (Brücke), presumably because then the new irritation exerts its influence at a time when the eye has just recovered from the effect of the preceding; the complementary after-images (see below) co-operate in bringing about this effect (Brücke).

The brighter and larger the images which are formed on the retina, the shorter is the time necessary for their perception, yet the time required only diminishes in arithmetical, though the intensity of the illumination and the size of the retinal image increase in geometrical, progression. The most sensitive part of the retina lies further from the centre of the retina than that part which perceives most rapidly the outlines of objects (Exner). The curve which represents the excitation of the retina presents a rise and a fall, so that when the illumination lasts a very short time, the full perception of the luminous impression does not occur (Fick). When the eye is continuously illuminated, the falling part of the curve indicates exhaustion of the retina. The absolute brightness of the light has no influence on the relative fatigue; the effect of this fatigue is the same as if the objective light were diminished in intensity by a fraction of its whole amount (Helmholtz). Fatigue increases most rapidly at first; the loss of light due to fatigue amounts in the first seconds, during which the luminous impression lasts, to more than 7 per cent. of the total amount; later, however, the loss is relatively much less. The whole loss during exposure for a whole day amounts to about 51 per cent., because the eye has continuous opportunities for restoration. In the morning the influence of fatigue is greatest (Fick, and C. F. Müller). In the centre of the retina the influence of fatigue is sooner developed than at the periphery (Aubert).

Quality of Luminous Impressions.

All the vibrations of the ether do not possess the power of exciting the end-organs of the optic nerve. Those the wave-length of which is greater than corresponds to Fraunhofer's line A (ultra-red heat rays) are unable to excite them, and are, therefore, invisible: those the wave-length of which is shorter than corresponds to the line H (ultra-violet chemical rays) exert so feeble an action

that peculiar arrangements are required in order to make them manifest.

The power which the different colours of the spectrum possess of exciting the retina is different. For the perception of yellow, a shorter illumination suffices than for violet (Vierordt, Burckhardt, and Faber), whilst red requires the longest illumination (Lamansky). The maximum degree of stimulation is, on the other hand, reached earliest in the case of red (Kunkel). The invisible character of the ultra-red rays has led to the investigation of the *diathermancy* of the media of the eye, and it results that the latter absorbs above 90 per cent. of the heat rays (Brücke, Janssen). In relation to the separate portions of the spectrum, the diathermancy of the media of the eye behaves as that of water (Franz); they therefore allow a sufficient number of the ultra-red rays to pass, to lead one to ascribe their not being perceived to their incapability of exciting the retina. The ultra-violet rays, which are seen with difficulty, appear of a lavender grey colour when they have been rendered artificially visible by removing the remaining portions of the spectrum (Helmholtz); the most external rays of the very long spectra of metals have no perceptible colour (Mascart).

The vibrations of the ether which are capable of exciting the retina give rise to the sensation of light by being propagated from the end-organs in the retina to the central organs in connection with the optic nerve.

The *intensity* (height of wave) of the waves determines the intensity of the luminous impression; the length of the waves, however, determines the specific peculiarities of the luminous impressions, to which we give the name of *colours*. The solar spectrum, which allows rays of all wave-lengths capable of affecting the eye to reach it simultaneously, exhibits all colours arranged side by side. In addition to these, which we denominate 'simple,' there are others which we term 'mixed' colours. The consciousness of the impression produced by a mixed colour is the result either of the union of rays of different wave-length (different simple colours), which have united so as to form a resulting wave-system which strikes the retina; or of a simultaneous excitation of corresponding fibres of the optic nerve by several rays of different colour.

In both cases the same simple colours give rise to the same mixed colour.

The sensation produced by the absence of any luminous impression upon a part of the retina which is sensitive to light is called 'black'; the colour of undecomposed sunlight is called 'white,' whilst 'grey' is white of less intensity.

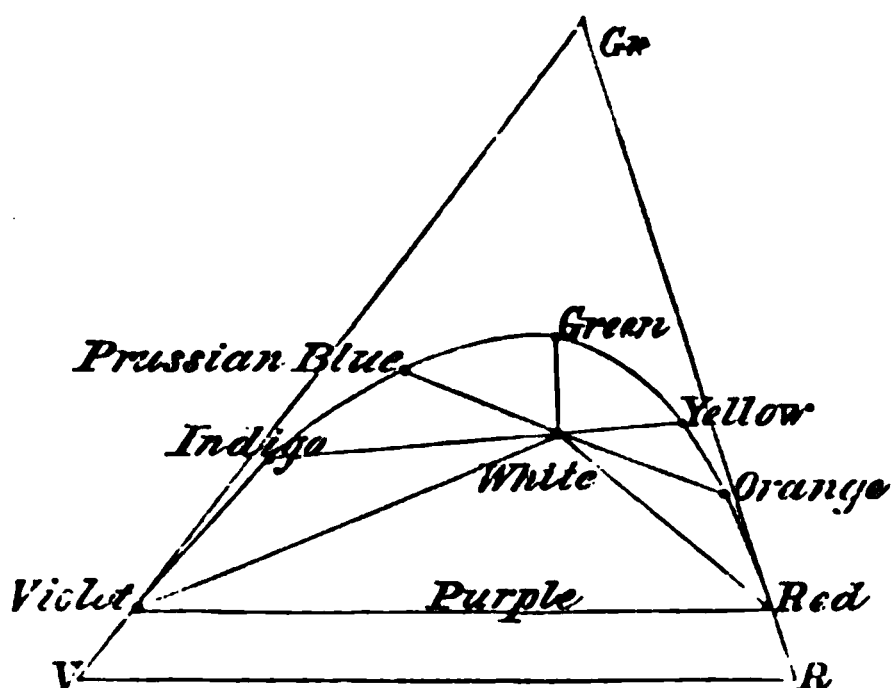
We may realise the two modes in which colours are mixed in the following manner: 1. Formation of a system of waves of different wave-lengths. *a.* The source of light itself furnishes such a system, which is decomposable by a prism into simple colours. *b.* The same effect results when luminous rays proceeding from several points strike the eye so as to fall upon the same spot in the retina. Simple means of effecting this are the following: a colour is looked at through an obliquely-placed glass plate, which at the same time throws, by reflexion, another colour into the eye (Helmholtz), or, in Scheiner's experiment, which was previously referred to, two differently coloured glasses are placed in front

of the two small apertures; in this case the two luminous cones are differently coloured. If the observing eye be now so accommodated that the two circles of diffusion partly cover one another, that part of the retina which is common to both is illuminated with a mixed light (Czermak).

2. Excitation of the same or of corresponding elements of the retina by different colours. *a.* The property which the retina possesses of retaining for a time luminous impressions is made use of, and different colours are allowed to fall into the eye in very rapid succession (the apparatus known as Newton's disc is made use of in this experiment); in this way the effect of the first excitation is still present, when the second commences to operate. *b.* Different colours are allowed to fall upon two 'corresponding points' in the two eyes.

Experiments conducted upon the perception of colours and upon mixed colours (Newton, Grassmann, Helmholtz, Maxwell) have led to the following laws: 1. The same impression of colour may be produced by very different combinations of colours; the number of possible colour-perceptions is therefore much smaller than that of the possible objective wave-forms. 2. Each colour appears whiter, the more intense the illumination, and when the illumination is most intense it appears white; of all colours yellow is the one which most easily passes into a white. 3. A combination of two simple colours of the spectrum gives rise to an impression, which can in every case be reproduced by a colour lying between them in the spectrum, mixed with a certain quantity of white (*i.e.* undecomposed sunlight), or it may be reproduced by white

FIG. 48.



alone (in the latter case the two colours are called *complementary colours*); hence it follows that even three or more colours of the spectrum when mixed always produce an impression, which can be reproduced by one of the colours of the spectrum mixed with white; any luminous impression whatever may therefore be produced by one of the colours of the spectrum and white.

In order to make the third law universally applicable, we must consider the spectrum to be in the form of a closed ring, a new colour being interposed

between the red and the violet ends, this being a compound colour, viz. *purple*, resulting from the mixture of red and violet. If in the middle of this closed field (fig. 48), white be placed, and if the field be so coloured, that every vector contains the combinations of one of the spectral colours with white in all proportions (so that the colour as it approaches the white always becomes whiter), a diagram is obtained, which immediately tells us what impression will result when any given colours are mixed. Let us, for example, imagine that at the points which correspond to the coloured components masses are placed, the magnitude of which corresponds to the intensity of the components, and let the centre of gravity of these (which must naturally lie within the field) be found; its situation will represent the luminous impression sought for. It is then seen that the coloured impression produced by the spectral colours corresponds to a spectral colour which lies between the component (elementary) colours, mixed with white; further, that the mixture with white becomes more intense the more diametrically opposed the two ingredients; lastly, that each shade of white unites two complementary colours.

The form of the including curve and the situation of the white must therefore be so chosen that the latter always lies in the line of union of two complementary colours, and indeed always lies nearer to that colour which must be represented relatively more intensely in order to form white with its complementary colour.

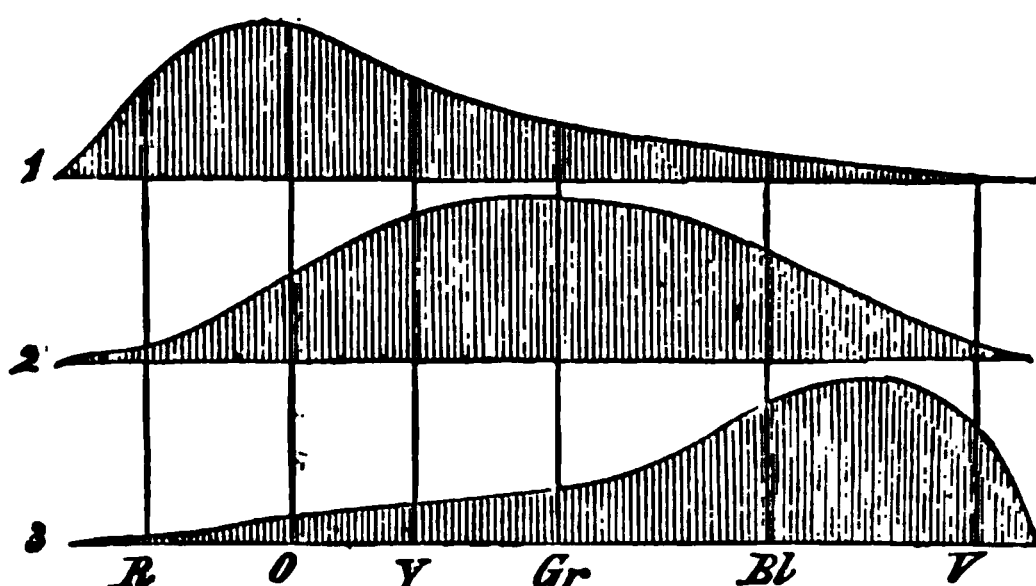
If we supposed that every fibre of the optic nerve were differently excited by different colours and so occasioned different luminous impressions, not only would the principle of 'specific energies' be contradicted, but many of the observations which have been referred to, especially the identity of the impressions perceived when the same colours are mixed objectively and subjectively, would be absolutely incomprehensible. All difficulties are, on the other hand, set aside by the hypothesis of Thomas Young and Helmholtz, that each spot on the retina contains a number of nerve-terminations, of which each one is capable of being excited by one particular colour and is able, by transmission through a nerve-fibre in connection with it, to occasion the consciousness of a particular coloured impression. A compound colour would then be decomposed (just as a musical sound is decomposed by resonators, or like light by a prism) into its components, which would excite the corresponding fibres. Admitting this hypothesis, the same impression would naturally result whether a compound colour, or each of its separate components, fell upon the retina, or if the components fell in rapid succession upon the retina, or even were distributed upon corresponding points of the two retinæ. According to this hypothesis, white would be perceived when all the retinal elements were equally excited.

It is impossible to determine *a priori* how many of these colour-perceiving retinal elements must be associated with each spot on the retina; the smallest number which can be assumed is three (Young). For reasons which cannot here be discussed, it is usually assumed that there must be present elements capable of perceiving red, green, and violet. Probably the number is actually much greater.

The most recent anatomical investigations have almost certainly demonstrated, that the *cones* are the elements in the retina which are concerned in the perception of colour (M. Schultze). These *cones* must, however, be looked upon as collections of nerve terminations; they appear to be longitudinally striated, and they pass into a thick fibre (cone-fibre), which consists of a bundle of the finest axis cylinders, which separate in the granular layers of the retina. The power of perceiving colours possessed by different parts of the retina varies according to the distribution of cones in them. The rods are in all probability merely endowed with the power of determining the quantity of light. They are connected with a single axis cylinder, or at least with a far smaller number of axis cylinders than the cones.

The hypothesis which has already been referred to in the text, viz. that each of the fibres supposed by Young to exist, is excited not merely by one, but by all colours, only in different degrees, explains the observation referred to at p. 389 in discussing the second law. In fig. 49 the ordinates of the curves indicate the

FIG. 49.



relative degree of stimulation which each of Young's fibres undergoes under the influence of each of the primary colours of the spectrum. 1 is the curve which represents the excitability of the fibres which are specially sensitive to red rays; 2, of those which are sensitive to green rays; 3, of those which are sensitive to violet rays.

As when the intensity of the illumination increases, the stimulation must soon attain a maximum, it follows that an intensely illuminated colour must excite all three fibres to a maximum degree, therefore equally strongly, and that therefore a sensation of white must result. Yellow, which, as the curves show, excites almost to an equal degree the three kinds of fibres, must most easily pass into white. In the colour-plane (fig. 48) places must be given to coloured impressions which correspond to the excitation of the individual fibres of Young, outside of the coloured field, viz. at R, Gr, and V; then, as fig. 49 shows, no objective colour exists,

which merely stimulates a single fibre of Young. Naturally again white must lie in the centre of gravity of three equal masses placed at R, G and V. The triangle R G V includes all *imaginable* coloured impressions, but the inner field alone contains those which are *possible* in the case of objective illumination; the remaining colours can only be developed subjectively.

The theory of Young, Helmholtz and Schultze is moreover supported by the following facts in addition to those previously referred to (viz. the results of mixing colours; the form of the fibres of the cones and rods); 1. In animals the habits of which are nocturnal (owls, bats) the cones are wholly wanting, and rods alone are present (M. Schultze); this fact agrees with their supposed function of merely appreciating differences in the quantity of light (light and darkness). 2. The power of discriminating colours is, in the eye of man, most developed in the *fovea centralis*, where cones alone are present, and diminishes towards the periphery in proportion as rods occur, ceasing entirely at the periphery, where the cones only occur in isolated situations (Aubert, M. Schultze). Here a qualitative irregularity in the perception of colours is discovered (see below). 3. Very frequently there exists an abnormality of the eye, to which the name of colour-blindness or blindness for red (Daltonism) is given. This abnormality consists in this, that red appears black, and that mixed colours which contain red appear as if the red were absent (white for instance appears greenish-blue). This condition cannot be explained otherwise than by supposing an absence, or a functional incapacity, of the retinal elements concerned in the perception of red. As some colour-blind people do perceive very intense red, it follows that we must assume not an absence, but an imperfection of these elements, of which there may be many gradations. The peripheral parts of the retina are normally to a certain extent colour-blind for red, and are so, according to Woinow, for green also. White is seen on those parts of the retina of a greenish tint. Moreover, when we try to ascertain the limits of the sensitiveness of the eye to colour, as for example the power of perceiving a very small coloured image or one imperfectly illuminated, red appears to be the colour which is least easily perceived (Aubert, Lamansky); it would thus appear that the cones which are sensitive to red require a stronger stimulus than the remaining cones, and further that in order that a colour be perceived, it is necessary that a certain number of cones be excited; these two suppositions are sufficient to explain all the known phenomena (still even a green colour-blindness can exist, Preyer).

When electrical currents are passed through the optic nerve, weak luminous sensations result; the field of vision appears of a violet colour with an ascending, and reddish-yellow with a descending, current (Ritter). This action manifests itself when coloured

objects are looked at, by an addition of violet or yellow to their proper colour.

The excitation of the fibres which are sensitive to violet rays appears therefore to be stronger with an ascending current, and weaker with a descending current, whereas the fibres which are sensitive to green or red are but slightly affected.

The yellow colouring matter of the *macula lutea* causes the centre of the retina to be more sensitive for yellow and less sensitive for violet, as many facts teach us (Maxwell, Preyer). The yellow colour of the field of vision, which comes on in cases of poisoning by santonin, has been explained by some (M. Schultze) as due to an increase of the yellow pigment, whilst others (Hüfner) imagine that it depends upon a paralysis of the fibres which are sensitive to violet, especially because, as a first effect, the field of vision is coloured violet—a phenomenon which is to be explained on the supposition that there is a preliminary stage of irritation which precedes the stage of paralysis of the fibres.

The manner in which light of different colours is decomposed in the cones cannot yet be understood (see below). But birds are provided with an apparatus which throws some light upon the function of the cones in the perception of colours. The cones of the retina of birds are simple elements, being only connected with a single, simple axis cylinder, and are therefore, according to Schultze's theory, really *rods*: these rods present, however, at the junction of their inner with their outer segment (see below) a spherical fatty body, which in the case of some is red, in that of others yellow, or even colourless. It is conceivable that the rods of the first kind only transmit red, those of the second yellow, those of the third perhaps white light. The perception of colours appears therefore, even in this case, to depend upon several rods, each kind being excited by light of a particular colour; this combination of rods corresponds to a single cone of the human retina (M. Schultze). In the retina of the owl the pigmented rods, above referred to, are absent, the only ones present being colourless.

In both rods and cones two constituent parts (segments), an inner and an outer, can easily be distinguished (M. Schultze). The external segment is essentially the same in both rods and cones, being merely longer in the former; it is regularly rod-like, it refracts light strongly, and is most strongly coloured black by perosmic acid; it constitutes a reflecting arrangement. The internal segment differs in the rods and cones; in the former it possesses the same thickness as the external part, in the latter it is fusiform and longitudinally striated; it is apparently of a purely nervous nature. The line of demarcation between these two segments is sharp, and here the rays coming from within must, in great part, be totally reflected. The light which penetrates the external portion of the rods and cones is either absorbed by the choroid coat

or again reflected towards the inner portions. Seeing that in the retina of birds the pigmented granular bodies are situated at the point of junction of the inner and outer segments of the rods and cones (while in other animals also refracting apparatuses of elliptical or lenticular form occur in the same situation), it is highly probable that the external segments are the specific light-perceiving organs. These present in all animals a transverse cleavage into fine plates, which are 0.0006^{mm} thick in doves, and 0.002 — 0.008 in crabs (M. Schultze). This peculiar structure has led to the hypothesis that the external segments have the property of changing by reflection against these plates the progressive light-waves into stationary waves; the latter would act in such a way that the maximum point would not coincide in the case of the different colours, but that individual colours would excite different points of the organ, an effect similar to that required by Young's theory. That stationary waves corresponding to all the different wave-lengths may be generated appears possible from the fact that not only the distance of the reflecting surfaces (thickness of the plates), but also the refractive index of the different plates in a rod, vary.

Images.

It has already been stated that from every point in an object the corresponding point in the image can be obtained by drawing the visual ray which joins them. It is in this direction too that consciousness refers to the exterior the cause of every luminous impression which originates in consequence of the irritation of a retinal element. It will be shown subsequently to what distance on this line the point of the object is referred. In the first place, let us now consider the case in which the transfer is effected in such a manner that all the points of the object appear to lie in a plane floating before the eye. This plane is called the 'field of vision.' As consciousness is continually forming a representation dependent on the state of irritation of all the retinal elements according to their real arrangement in space, it happens that a *field of vision* is always being seen; this appears 'black,' as long as every cause of irritation is wanting. To every excited retinal element there corresponds a luminous point, and to every unexcited element a black point, at diametrically opposite points of the field of vision. The latter then is filled with exactly the same, but inverted, images as are objectively present on the retina. As the latter are, in relation to the objects seen, inverted, the objects are seen erect in the field of view.

The blind spot does not occasion any perceptible gap in the field of vision. The want of optical excitation (the consciousness of which we designate by the term black) can only be perceived where terminations of nerves sensitive to light are present. But

there are no such terminations in the blind spot. The latter therefore behaves towards light as any spot on the skin would do; we do not experience with the hand any sensation of black, although no luminous impression proceeds from the hand. As the visual impressions of the contour of the blind spot are by means of the visual rays localised in the field of vision, consciousness must logically perceive the want of intermediate luminous points, and appears to conceive them according to the rules of *probability* (E. H. Weber). In this way we may probably explain the experiment described at page 399, in which the place of the object which has disappeared is taken by the colour of the ground and not by a black spot. The white colour of the paper here fills up the gap as the most probable substitute.

As every point in the retina merely contains a definite number of terminations of the optic nerve (rods or cones), any image can only consist of a limited number of luminous impressions separated from one another in space and forming a kind of mosaic or embroidery pattern. But the mosaic is so fine that there may result an impression as of a continuous drawing. The same object must appear sharper, the greater the number of sensitive retinal elements over which its image is distributed. Hence the sharpness with which a given object is perceived depends (1) upon the magnitude of its retinal image; the same object will therefore appear sharper when near than when distant; (2) upon the situation of the retinal image, for the sensitive retinal elements are most thickly pressed together in the *fovea centralis* and the *macula lutea*, whilst they are most sparsely scattered near the borders of the retina. An object, therefore, which is situated at the same distance will be seen most sharply when its image falls upon the centre of the retina; hence when the eye looks most keenly at (*i.e.* is fixed upon) an object, it is so turned that the latter throws its image upon the middle of the retina, on the *fovea centralis*. The visual ray which strikes the *fovea centralis*, *viz.* the axis of vision, does not absolutely coincide with the optic axis of the eye, but is bent backwards and a little outwards and downwards from the latter. The two form an angle of $3^{\circ}5-7^{\circ}$ with one another.

This deviation of the two axes can be recognised and measured by causing the centre of a horizontally-placed measuring rod to be fixed by the eye observed; at one end of the rod is a light, at the other the eye of the observer. The three luminous reflexions which were previously referred to in describing Mariotte's experiment do not then appear in symmetrically similar order if the observer and the light change places: the symmetry is only restored when the observed eye is fixed, not upon the centre, but on a point somewhat to the inner side of the centre, of the measuring rod. The symmetry is even then not absolutely perfect, because the centring of the three refracting surfaces of the eye is not absolutely true.

An object will further not generally be recognisable, unless its retinal image covers a sufficient number of sensitive retinal

faces naturally are at some distance one from the other, it may possibly occur that in central sight minute points, as stars, form images which fall in the space between the cones, and so disappear. This actually does occur (Hensen).

For the perception of small images the mode of disposition of the mosaic of retinal elements is not without importance; in the yellow spot it is in the rhombic figures formed by the intersecting of neighbouring circles that the cones are situated (M. Schultze).

The details of an image are distinguished partly by the difference in brightness, partly by the difference in colour. In the latter case the delicacy of the power of perception does not depend upon the number of the retinal elements, but upon the number of the elements capable of appreciating colour which are covered by the image. In the centre of the field of vision the two circumstances co-exist, as in this situation cones only exist; towards the periphery, however, the power of distinguishing colours diminishes far more rapidly than the power of discriminating differences in luminous intensity.

Subjective Images and Optical Illusions.

As nervous arrangements play a part in the perception of light, as of all other sensations, modifications of nervous excitability must make themselves felt in connection with them, and lead to abnormalities or *illusions*. The same vibration of the ether will, for instance, give rise to a strong or weak impression, according to the degree of excitability of the end-organs of the optic nerve, or of its fibres, or even of the central organs connected with them. Other circumstances lead to actual errors, to a perception of a luminous impression independent of rays of light, or to the perception of other rays than those which are actually present (colour-illusions). Such impressions we call 'subjective.' The most frequent are the following:

1. *After-Images*.—A fibre of the optic nerve having been excited, persists in its excited condition for some time after the exciting luminous ray has ceased to act, and the continuance is long and intense in proportion as the primary excitation was long and intense. In consequence of this, after every luminous impression, the object which has been seen remains visible for a very short time—an *after-image* being seen. Upon the property which has been alluded to depends the appearance of a fiery circle, which is seen when a burning coal is swung in a circular path before the eyes. The following instruments are based upon the existence of persistent images. The Thaumatrope is a disk rotating in front of the eyes, near the circumference of which a body which is continually moving is represented in the different successive stages of its movement, so that each figure can be perceived for a moment; each impression then persists until the following one succeeds it, and in this way the movement appears continuous.

The *coloured rotatory disk* (Newton's disk) is a disk turning with rapidity and divided into sectors of various colours; the colour of one sector persists during one whole rotation, so that a mixture of many colours is presented to consciousness. If the original luminous impression is strong, the persistent (or secondary) image is at times dark, *i.e.* the excitability of the fibres has been for the moment diminished by fatigue, so that a dark place, having the same situation as the bright object seen at first, appears; this is called a *negative after-image*. At times positive and negative secondary images alternate for a period, *i.e.* the momentarily abolished irritability returns for an instant, so that the (positive) secondary image appears, to disappear again, &c. The secondary images offer some peculiarities when the primary impression has been due to an intense light or to a prolonged luminous impression. These images do not then appear of the same positive colour, but often of another *contrasting* colour, and often pass from one to the other successively. The contrasting colour is always that one which, if added to the primary colour, would give the tint of ordinary daylight (which is not pure white, but a little red), and therefore the 'contrasting' is very nearly the same as the 'complementary' colour (Brücke).

Even white light appears after a luminous impression, amongst the 'contrasting colours'; if, for instance, we place a coloured piece of paper on a white surface, and stare fixedly at it for some time, and then look at the white surface, there appears a secondary image possessing the form of the coloured piece, but of the contrasting colour. The phenomena of contrast may be explained by supposing the exhaustion of the retinal elements which correspond to the primary colours.

Secondary coloured images appear also after impressions produced by white light, when these have been very intense (after looking, for example, at the sun); ordinarily a succession of divers colours appears, sometimes positive and negative colours alternating. This phenomenon of successive contrast of colours is probably explained by the excitation of the individual colour-perceiving elements lasting for different periods of time after the luminous impression has acted. In the peripheral parts of the retina these *contrast-phenomena* are modified by the red-blindness (and green-blindness), which are characteristic of these regions (Adamük and Woinow).

2. *Irradiation* becomes perceptible when a bright object on a dark ground is looked at; the object then appears to be larger than it really is—conversely, a dark object on a bright ground appears smaller. This phenomenon results from defective accommodation, whereby the bright objects furnish blurred images.

Consciousness, under these circumstances, is inclined to add to the predominating part of the image the half-illuminated fringe

(which is equal in width to the radius of the diffusion-circle); now, on the one side brightness predominates over shade, and on the other the object over the ground beneath it. If the ground is black and the object white, the latter appears larger at the cost of the former; if, on the other hand, the object be black and the ground white, the second influence can preponderate so much over the first, that even black lines appear broader at the expense of the white ground (Volkmann).

3. *Simultaneous contrast* includes a series of phenomena which depend upon the comparison of two colours or tints bounding one another in the field of vision, as well as the illusion which results therefrom.

A white field appears the brighter, the darker its immediate surroundings (a white trellis-work upon a dark ground exhibits at the points of intersection apparently dark spots, for here the surroundings of the white spots contain less black than the remaining parts of the trellis); similarly, a colour appears the more intense, the more completely are its surroundings destitute of it, *i.e.* the nearer the surrounding medium approaches a *contrasting colour*. Conversely on a (feebly illuminated) white surface those components of white come out most strongly which are wanting in the vicinity; white thus appears in the contrasting colour of the vicinity (the shadow of a rod illuminated by a candle appears in daylight not white or grey, but is of the contrasting colour to the yellow candlelight, viz. blue).

The many examples of actions of simultaneous contrast which occur cannot here be referred to. Phenomena of contrast do not appear upon wholly unexcited places of the retina, so that the so-called *associated-sensations* are in no way identical with them (Rollett).

4. Amongst subjective phenomena are further to be mentioned the illusions as to colour which originate through the peripheral colour-blindness and the unequal excitability of the organs engaged in the perception of colours, *e.g.* very rapidly intermitting white light, as the luminous impression does not last long enough to excite the retinal elements which are sensitive to red, appears greenish (Brücke).

5. Excitations of the light-perceiving retinal elements due to causes which are purely internal, without external influence. To this class belong: *a.* Mechanical irritation, brought about by the circulation, and which only occurs where there is morbid irritability; under these circumstances appearances of sparks, lightning, &c. may be seen; sometimes there appears, especially before sleep, a complete image of the retinal vessels, with their contained blood-corpuscles, &c. *b.* Central excitations of unknown origin and manifesting themselves in the most diverse forms ('hallucina-

tions,' 'phantasms'); these are seen especially in dreams, in the half-waking state, before going to sleep, and in diseased conditions even during the waking state.

Entoptical Perceptions.

'Entoptical' phenomena are to be clearly distinguished from such as are subjective. Entoptical phenomena are visual impressions of objects which are present within the eye itself. The most important of such phenomena are: 1. Perceptions of opacities and obscurations of the refracting media of the eye. These are apparent when, by illuminating the eye, their shadows fall upon the retina, and they are best seen when parallel luminous rays traverse the eye.

They appear in the form of dark spots, balls, streaks, rows of pearls, &c.; in part, they are fixed, in part (those of the vitreous humour), they change their position, especially during sudden movements of the eye or of the head.

2. Perceptions of the retinal vessels, brought about by their shadows falling upon the layer of rods. In order to bring out these shadows they are directed upon the lateral parts of the retina, which are seldom lighted up, by causing an intense light to fall upon the transparent sclerotic, or the shadows are made to move by causing a luminous point to pass backwards and forwards before the eye. Under these circumstances a dark delineation of the vessels, on an illuminated field, is perceived; even the border of the *fovea centralis* is recognisable by a shadow (Purkinje's figures).

3. The perception of the blood-corpuscles in the retinal capillaries, when the eye is very feebly illuminated (as by a layer of snow, a lamp-globe, or (Grünhagen) a dark blue glass held before the sun); this phenomenon is, as yet, not fully explicable.

4. Haidinger's brushes. When polarized blue light or polarized light containing blue rays falls into the eye (as, for instance, when one looks at the sky through a *Nicol's prism*, or even with the naked eye, as the blue rays of the sky are already polarised), a brush-like figure is observed, which moves with the eye. The cause of this figure is to be sought for in the presumed doubly-refracting fibres of the yellow spot, which when impinged upon by polarized light at various angles, absorb in one place more, in another less, and so give rise to the above-named phenomenon (Helmholtz).

Movements of the Eye.

The eye is capable of very extensive movements in the orbit, and the absolute mobility of the organ of vision is considerably increased by that of the head as a whole. Hence it is possible in any position of the body to observe objects in all situations of space, *i.e.* so to place the eye as to cause the retinal image of any object to fall on the *fovea centralis retinae*. The great mobility of the eyeball depends upon the mode of its attachment to the orbit. It rests on the pad of fat of the orbit, as the head of a bone in a ball and socket joint rests in the hollow cavity, and it can therefore rotate around innumerable axes. These movements, which are effected by the muscles of the eye, are held in check, firstly, by the points of attachment of antagonizing muscles, and, secondly, by the attachment of the optic nerve. In addition to the movements of rotation, changes in the position of the globe as a whole can occur

in consequence of the yielding nature of the surroundings—in this case ‘the joint-cavity is displaceable’ (Ludwig).

The point of rotation of the eyeball does not lie, as was surmised *à priori* and as was concluded from researches (Volkmann), in the middle of the visual axis, but (Donders and Doijer, Fick and Müller) in the case of normal eyes 1.77^{mm} behind it.

It is to be noticed that when the eyelids are forcibly opened, the eyeball protrudes somewhat from the orbit, probably by the contraction of both the oblique muscles; the movement forwards is most marked when the eyes look horizontally or downwards, and then it amounts to about 1^{mm} (Fick and Müller).

To understand the changes in the situation of the globe and the arrangement and mode of action of its muscles, we must assume the existence of certain fixed points and lines in the eyeball, the changes in the situation of which furnish a measure of the movements of the eye. One line in the eye is given by its anatomical construction, viz. the *visual axis*, which is the *principal ray* proceeding from a fixed point, the situation of which in relation to the optic axis has already been referred to (p. 409). Starting from the *fovea centralis*, which may be considered to be one pole of the eyeball, two meridians at right angles to one another may be drawn on the retina. Their position is determined by certain physiological properties of the eye; they divide the retina into four quadrants which have in the two eyes certain reciprocal relations, and they are called *lines of separation* (one of which is horizontal, the other vertical).

If we now imagine a plane passing through the eye at the centre of the visual axis and perpendicular to it, it will cut the spherical surface in a great circle perpendicular to the meridians, which we designate the *equator* of the eye, the plane being termed the ‘*equatorial plane*.’ We have then three great circles perpendicular to one another (the equator and two meridians); the planes corresponding to these circles intersect one another in three diameters at right angles to one another; these are: one sagittal (the visual axis); another vertical, and a third horizontal. These may be employed as a system of co-ordinates movable with the eye and indicating its movements. A second system of co-ordinates absolutely fixed in space, and coinciding with the movable system when the eye is in its position of rest, must also be assumed to exist. In any other position of the eye two or three of the corresponding axes of the two systems must form angles with one another.

The movements of the eye are especially of importance in bringing about the combined positions of the eyes and are limited by the latter. That position is assumed as the *position of rest*, from which all movements may be supposed to start. This so-called ‘*primary position*’ is one in which all three axes of one eye are

parallel to those of the other, and the transverse axes lie in one straight line, the visual axes being therefore antero-posterior (sagittal) from within outwards.

It is obvious that this position can be associated with a voluntary *inclination* of the visual axes to the horizon. Amongst all such possible positions there is one to be mentioned as a *primary position*, properly so called, namely, that inclination in which convergent movements of the visual axes may occur without the eyes requiring visibly to rotate around their visual axes, as is the case in all other positions. The determination of this inclination will be given below. It has now been established (Listing, Meissner, Helmholtz) *that when the eye moves from the primary position, its movements take place around axes situated in the equatorial plane (so that the visual axis is always perpendicular to the axes of rotation and that rotations never take place around the visual axis)*. Amongst the innumerable axes which may be supposed to exist in the equatorial plane, there are two which are first to be mentioned, viz. those which are at the same time co-ordinate axes, viz. the transverse axis and the vertical axis. Rotations around these two axes lead to the '*secondary positions*' of the eye. Rotation around the first merely occasions an alteration of the inclination towards the horizon and the parallelism of the axes continues; rotation around the vertical axes produces a rotation inwards or outwards, and consequently a convergence or divergence of the visual axes, the inclination to the horizon continuing the same. Thus in the first case the plane of vertical separation, but not that of horizontal separation, coincides with that which corresponds to it in the fixed system of co-ordinates; in the second case the converse is true.

Rotations around other axes lying in the equatorial plane of the eyeball lead to '*tertiary positions*' of the eye. As every such rotation can resolve itself, according to simple rules, into a rotation around the vertical axis and a movement around the transverse axis, it follows, in the first place, that tertiary positions are as much associated with convergence of the visual axes as with their change of inclination to the horizon, and, secondly, that neither the vertical nor the horizontal plane of separation coincides with the planes which correspond to them in the fixed system of co-ordinates; they are both inclined the one to the other. The eyes have therefore undergone in the tertiary positions *an apparent rotation around their visual axes*, in the same direction as the hand of a watch moves, when directed to the left looking upwards, when to the right downwards. Every position of the visual axes is therefore associated with a certain rotation of the eye, which can be deduced from Listing's law.

If α be the vertical and β the horizontal deviations of the visual axis from

primary position the vertical strongly-marked cross at p be looked at fixedly, so that an *after-image* is impressed upon the vertical and horizontal meridians, that image remains unaltered in the secondary positions (s, s_1), but takes up in the tertiary positions t and t_1 the situations given, appearing therefore oblique, and at the same time no longer rectangular, corresponding to the lines of intersection of the two meridian planes with the observed plane. If the cross at p were placed like the dotted cross, so that one of its limbs fell on the line pt , no distortion of the secondary image occurs at t . If the plane which is looked at be provided with horizontal and vertical lines, Listing's law may easily be proved and confirmed by means of the situation of the secondary images (Helmholtz).

The Muscles of the Eye.

The mode of action of each individual muscle of the eye, *i.e.* the position of the axis, around which, if it acted independently, it would move the eye, can be calculated, provided that the situation of its origin in the orbit and the position of its attachment to the bulb be known. The situation of these points is expressed by the length of the abscissæ cut off by the perpendiculars drawn from them to the three fixed co-ordinate axes.

The situation of the axis is determined by the three angles which it forms with the three co-ordinate axes of the eye in its initial position. In this way the following positions of the axes have been determined in the case of the six muscles of the eye (Fick); the initial position coincided approximately with the primary position.

Muscles	Angle which the axis of rotation forms with the		
	Visual axis	Vertical axis	Horizontal axis
Rectus superior . . .	111° 21'	108° 22'	151° 10'
„ inferior . . .	63° 37'	114° 28'	37° 49'
„ externus . . .	96° 15'	9° 15'	95° 27'
„ internus . . .	85° 1'	173° 13'	94° 28'
Obliquus superior . . .	150° 16'	90° 0'	60° 16'
„ inferior . . .	29° 45'	90° 0'	119° 44'

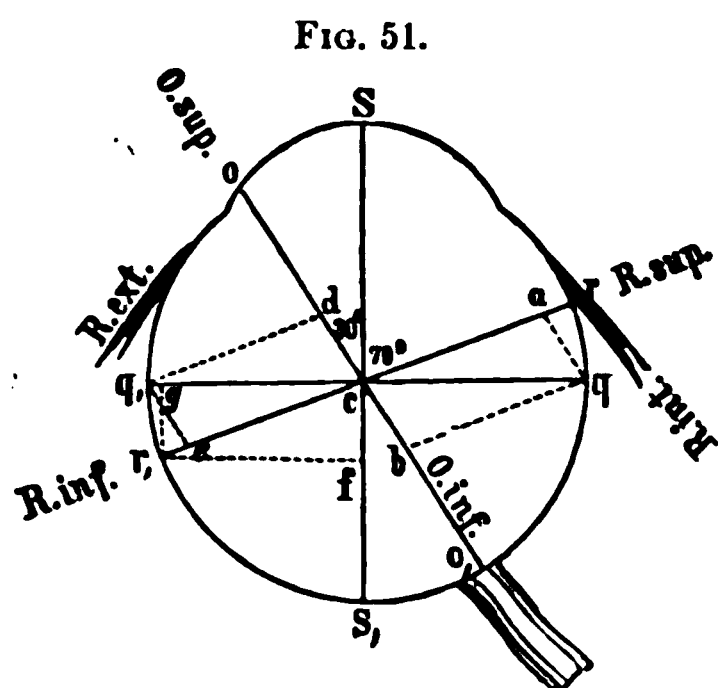
For the chosen initial position there does not exist, as may be seen, any axis of rotation in the equatorial plane of the eye, otherwise it would form a right angle with the visual axis. The axes of rotation of the internal and external recti are very close to the vertical axis, so that actually they rotate the cornea almost simply inwards or outwards. The axes of the two oblique muscles, on the contrary, are situated exactly in the horizontal plane, at each side of the visual axis, each being at a distance of about 30° from it, so that the superior oblique draws the cornea outwards and downwards, whilst the inferior oblique draws it outwards and upwards. The axes of rotation of the recti, superior and inferior, are considerably deviated from the horizontal axis, so that the former rotates the cornea upwards and inwards, the latter down-

wards and inwards. From the angles we conclude that each of the three pairs of muscles has approximately a single axis, and therefore acts almost antagonistically to the others.

As all the real movements of rotation of the eye are effected around the diameter of the equatorial plane, it follows that several muscles must co-operate in the production of almost any movement. This has actually been ascertained to be the case with eyes which have been partially paralysed.

Fig. 51 exhibits a horizontal section of the left eye; ss_1 is the visual axis, and qq_1 the transverse axis. This plane contains, according to what was previously stated, the axes of rotation of the recti rr_1 and of the oblique muscles oo_1 .

If the moments of rotation be expressed by lines corresponding to the axes of rotation, and drawn to the one side or to the other of the point of rotation, these moments of rotation may, in a manner quite analogous to the parallelogram of forces, be combined into resultant moments of direction; the diagonal of the



parallelogram gives by its direction the situation of the resulting axis of rotation, and the direction of the rotation, whilst its length furnishes the magnitude of the resulting rotating force. Conversely, rotations can be decomposed according to given axes. Thus the diagram shows that to produce a rotation of the bulb around the horizontal axis to the extent $c q$, the rectus superior and obliquus inferior must act together, and in the relations indicated by ca

and cb . For an equal rotation $c q$, in the opposite direction, the obliquus superior and the rectus inferior must co-operate in the relations indicated by the lines cd and ce .

Further, the figure shows that the rectus inferior by itself can bring about not merely a rotation around the horizontal axis cg , but also one around the visual axis (cf). The consideration and estimation of muscular action necessary to produce any given movement are such very complex processes, especially because as soon as the smallest changes in the position of a muscle have set in its axis of rotation has become altered, that the subject cannot here be pursued further.

The nerves which preside over the movements of the eyeball are, the oculomotor (3rd), the N. abducens (6th), and the trochlear nerve (4th). These nerves, which contain a large number of fibres, and the actions of which can be varied with great rapidity, are united on the two sides of the brain by a certain bond, which tends to limit the movements brought about under their influence.

This association leads, in the first place, to only such movements happening, as result in both visual axes being in the same plane (visual plane), so that when they are not parallel, if prolonged, they meet and intersect at a point ; they have, therefore, so long as the head is held erect, the same inclination towards the horizon, for the two points of rotation can be considered fixed. Further, their reciprocal inclination is limited, so that they only diverge to a very slight extent anteriorly, whilst they can converge to any required extent in so far as their position will admit of it. The mechanism by which this association of movements is effected is altogether a puzzle. Deviations from its normal condition constitute squinting (strabismus). The central organ, which co-ordinates the movements of the eye, is situated in the corpora quadrigemina.

Binocular Vision.

Normally the two eyes act together, and the advantages which result from this association are the following: 1. Correction of the faults of the one eye by the other. 2. The perception of space is more perfect, because when we look at an object from two different points of view, instead of observing a mere projection of it in a surface, its third dimension in space is appreciated. 3. A more accurate estimate of the magnitude and the relative distances of objects is formed.

Simple Vision.

Though we look at external objects with both eyes, these in general are seen as single ; this can only depend upon the fact that the excitation of certain associated spots on the two retinæ is referred by consciousness to the same point in space—or, in other words, that both eyes possess but a single, common field of vision, and that the luminous impression which originates by the excitation of two associated points, appears at one point in the field of vision. Such associated points are called *corresponding* or *identical* points. An object which is seen single by the two eyes, whatever their position, must therefore project its image on the two retinæ in such a manner that the two points of the image which correspond to one point of the object fall upon corresponding points on the retinæ. If one of the two eyes be deviated, to however small an extent, a double image must at once originate. We shall subsequently refer more in detail to the nature of ‘Identity.’

Situation of Corresponding or Identical Points. Horopter.

Concerning the relative positions of corresponding points, the following laws are apparent :

1. As an object c , which is looked at fixedly by both eyes, and the images of which fall, consequently, upon the terminations of the visual lines c and c_1 , is seen single, the two terminations of the visual axes c and c_1 must be corresponding points.

2. If the centre, c , of an object, which is seen single, be looked at, it follows, as the simple construction of the figure shows, that the identical points which correspond to all points of the right half of the retina, lie on the right side of the other retina also, and conversely. Further, that the upper half of the retina of one eye corresponds to the upper half of the retina of the other eye, and the lower half of the one to the lower half of the other.

Let the circles L and R represent projections of the two retinae,

FIG. 52.

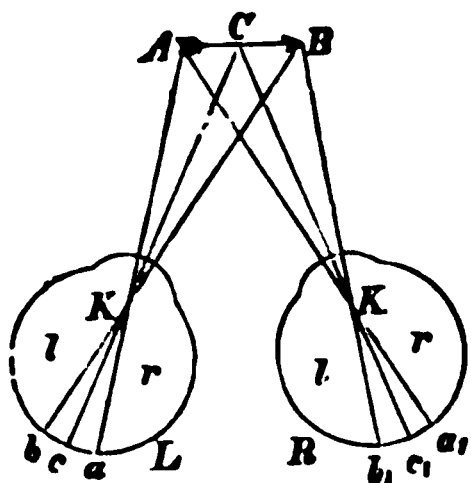
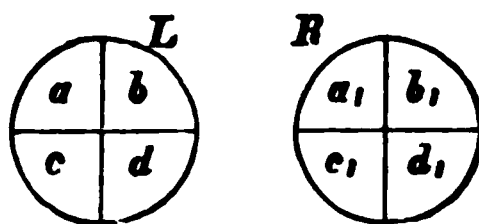


FIG. 53.



the similarly designated quadrants a , a_1 , &c., are corresponding. The two meridians which separate these identical quadrants are called lines of separation (vertical and horizontal).

3. It follows, further, that corresponding points on the two vertical lines of separation must be identical, and this is also true of points on the horizontal lines.

If in a given position of the eye the visual rays belonging to two corresponding points be drawn and prolonged beyond the eye until they intersect, the points of intersection will evidently be the points which in that position of the eyes appear single. The term *horopter* is given to the combination of all those points in space which, for any one position of the eyes, appear single. If the horopter had been perfectly determined for any position of the eyes, the relation in the position of corresponding points would obviously be likewise determined, and the horopter for any other position of the eyes might be constructed. Conversely, when the relation of the situation of these points is known, the horopter for any position of the eye can be deduced. In so far as the relative positions of the points, the most simple statement is the following: *If the two retinae, with their corresponding lines of separation, be imagined to be superposed, all the points which coincide, or touch, are corresponding points.*

This statement is not rigorously true, even if the form of the retina, which is not perfectly spherical, be taken into account. The vertical meridians are not perfectly identical, and the true vertical lines of separation do not exactly coincide with them, above being inclined outwards, and below being inclined inwards. The physiological vertical axis is therefore somewhat inclined to the geometrical axis.

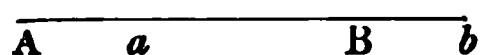
With the help of the above data the horopter can be determined mathematically or geometrically. The results of calculations are confirmed by experiments, and the latter establish the correctness of the relations in the position of corresponding points on the retinae.

A general deduction relating to the horopter can be arrived at by the following method (Helmholtz). Every point on the retina may be considered as a point of intersection of a meridian and of a 'parallel circle' (parallel circles being such concentric circles as pass around the *fovea centralis*, which is the pole of the retinal sphere). It is possible to calculate, 1, the 'meridian horopter,' *i.e.* the assemblage of lines of intersection of two planes passing through identical meridians, and the nodal points; 2, the 'circular horopter,' that is to say, the assemblage of the intersections of two conical surfaces passing through identical parallel circles and the nodal points; 3, the point-horopter, *i.e.* the horopter of corresponding points, which obviously is the intersection of the meridian and circular horopters.

A second method of deduction (Hering, Helmholtz) considers the plane of the vertical meridian as rotating around the vertical axis, and the plane of the horizontal as rotating round the horizontal axis; the sections of retina so obtained are termed longitudinal and transverse sections. Longitudinal sections which make the same angle with the plane of the vertical meridian are identical. The lines of intersection of the planes of corresponding longitudinal sections constitute together the 'horopter of the longitudinal sections.' Similarly, the identical transverse sections form a system of intersecting lines—the horopter of the transverse section. The intersection of the two horopters is the point-horopter sought for.

Both methods must, if rightly carried out, furnish the same results. Each method possesses special interest, for not only the point-horopter, but the line-horopter is of importance. This remark specially applies to the previously mentioned meridian

FIG. 54.



horopter. A straight line, which is fixed at one point, naturally forms an image of itself in a meridian of the retina. If now a line throws an image upon two identical meridians, it must appear single, even though its individual points do not fall upon identical

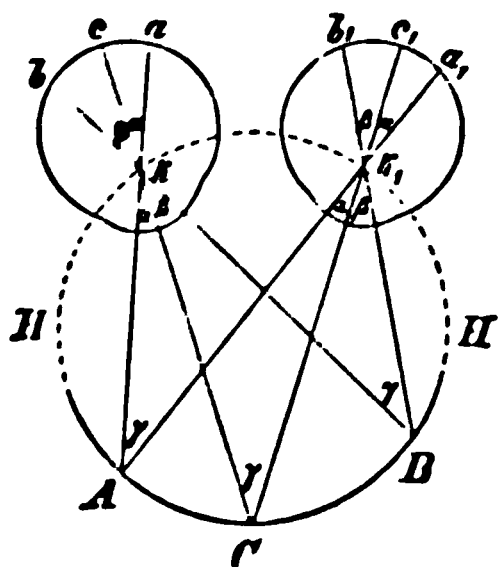
points, for the double images then are superposed in the field of vision, as the lines AB and ab in fig. 54. The meridian horopter or the normal surface (v. Recklinghausen) possesses the property that all straight lines falling upon it appear single, though all the points lying in it do not do so.

For practical purposes the second of the two methods previously referred to is more convenient, chiefly because it permits of our taking into account the deviation of the physiological vertical meridian. The results of the calculation cannot here be discussed, as an exhaustive treatment of the difficult problem of horopters would not be consistent with the object of this handbook, and instead of attempting it, those determinations of horopters will be treated of which can be arrived at by simple geometrical considerations.

1. *In the primary position, and in secondary positions when the visual axes are parallel and directed forwards*, the horopter is a plane parallel to the plane of vision passing through the point of intersection of the vertical axes of the two eyes. As it is the physiological vertical axes, however, which are here concerned, and as their point of intersection is situated about five feet below the field of vision, it follows that the plane of the horopter, which would otherwise be at an infinite distance below, is only five feet below the visual plane. If, therefore, we look horizontally into infinite distance, the ground constitutes the horopter-surface—a fact which is of great importance for sight in this position (Helmholtz).

2. *In secondary symmetrical positions, when the visual axes are convergent*, the horopter is as follows: two lines in the horopter

FIG. 55.



must be determined, viz. one which corresponds to the identical points in the horizontal lines of separation, and one which corresponds to the identical points in the vertical lines of separation (a transverse section of the horopter formed by the plane of vision, and a median section of the horopter).

(a.) *The transverse section of the horopter is a circle* (J. Müller). In fig. 55 the two transverse sections of the eyes pass through the horizontal lines of separation.

The transverse section of the horopter must therefore be in the plane of the paper (visual plane); c and c_1 are the extremities of the visual axes, c is the fixed point. If now for two points, as a and b in the horizontal line of separation, we seek the identical points on the other side, the latter must evidently, 1, lie on the same side of the termination of the visual axis; 2, be equally distant from the visual axis; they lie, therefore, at a_1 and b_1 . The visual rays

which belong to these intersect at the points A and B, which are therefore points in the horopteric line sought for. It is readily seen by looking at the drawing of the angles at the nodal points k and k_1 , that the angles at A, B, and C (γ) are equal. As they all proceed from the common points k and k_1 , they must be all peripheral angles of a circle $\Pi \Pi$, passing at once through k and k_1 . But as this is the transverse horopter-line sought for, the visual rays proceeding from all the other identical points on the lines of horizontal separation must here intersect.

(b.) The median section of the horopter, on the other hand, is a straight line, perpendicular to the visual plane, and therefore inclined to the horizon—the line in which the two planes which pass through the vertical lines of separation intersect. This is most easily understood if fig. 56 be drawn upon a piece of paper which is then cut through along the line $\Pi \Pi$, so that the two sides can be made to converge. The two sections of the eye pass through the vertical lines of separation in such a manner that the two converging planes which cut at $\Pi \Pi$ are the planes of the vertical meridians. It can be seen at a glance that the visual rays of all the points in the lines of separation which are equally distant from the terminal points c and c_1 of the visual axis, e.g. a and a_1 , b and b_1 , meet in points on the intersecting line $\Pi \Pi$, and that the latter therefore

FIG. 56.

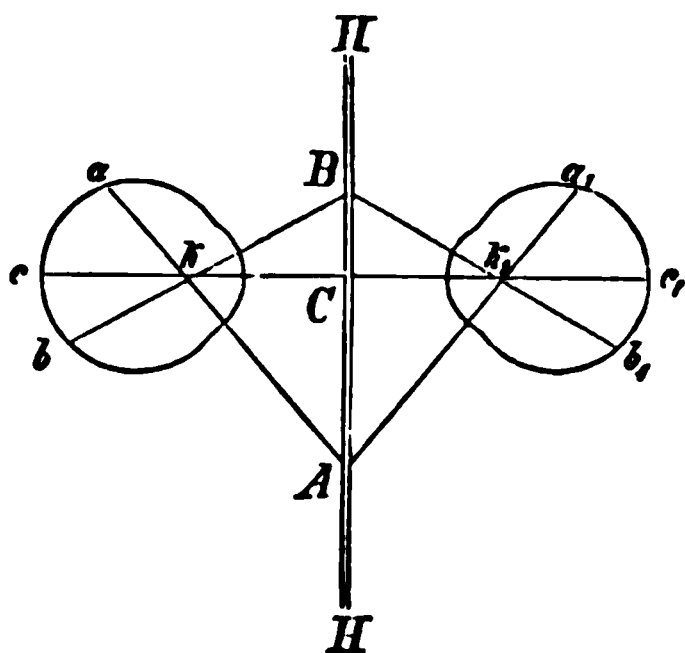
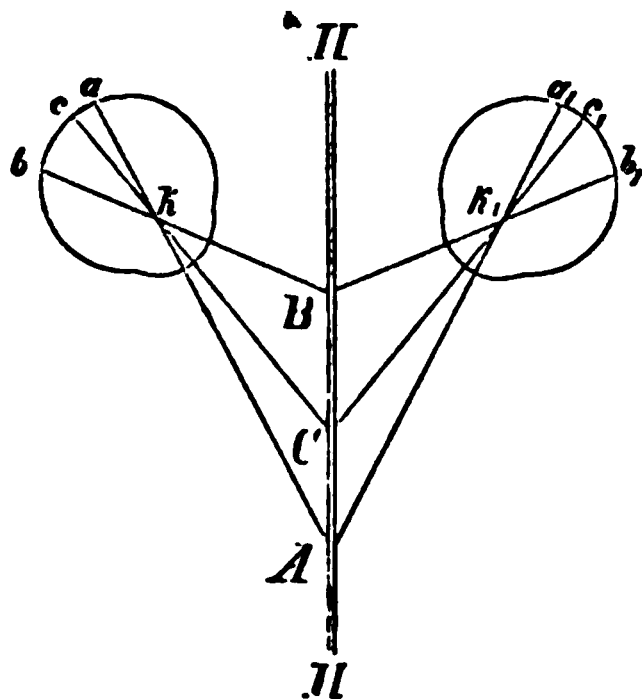


FIG. 57.



represents the median horopteric line. This horopter for the converging secondary positions is limited by the two lines just alluded to.

3. In (symmetrical) secondary positions accompanied by rotation (so-called tertiary positions) the vertical lines of separation, as well as the horizontal lines of the two eyes, meet at an angle. If now (a) a plane is made to pass through each vertical line of separation, the two planes intersect in a straight line, which is inclined to the visual plane (nearer to the eyes superiorly in tertiary positions, with these eyes inclined upwards, nearer to the

eyes inferiorly in tertiary positions in which the eyes are directed downwards. This inclined line, as well as the inclined position of the vertical lines of separation, are rendered evident by the annexed figure 57, which like 56 should be drawn upon a piece of paper, and be split up along $\pi \pi$. In the model $c c c_1$ is the visual plane, and $\pi \pi$ is the line of intersection of the two planes of separation, and which is inclined as in fig. 56. It is seen that the visual rays of all the corresponding points situated in the vertical lines of separation, for example a and a_1 , b and b_1 , intersect also in the line $\pi \pi$, and that this line represents in consequence the horopter of the vertical lines of separation.

(b.) If planes are made to pass through the horizontal lines of separation, these likewise cut in a line. The visual rays of identical points of the horizontal lines of separation, if they do intersect, could therefore only do so in this line. But if from any point in the latter two visual rays be drawn, these rays meet, as can readily be seen, in *symmetrical but not in identical* quadrants of the vertical circles of separation. Hence it follows that the visual rays proceeding from identical points of horizontal lines of separation do not in general intersect, in tertiary positions, and that for these there is consequently no horopter. In general, the horopter for tertiary positions, besides the meridian line, only includes another curve of double curvature passing through the fixed point, and which cannot be here considered.

Hitherto only symmetrical positions of the eyes have been discussed. It is impossible here to examine in detail the unsymmetrical positions in which the fixed point is at unequal distances from the nodal points. It is to be remarked that positions occur in which the fixed point alone forms the horopter.

In addition to the horopter of points which has hitherto been considered, the horopter of meridians or the normal surface, whose properties have already been referred to at p. 424, is to be mentioned.

This surface (v. Recklinghausen) in secondary convergent positions is a plane perpendicular to the visual plane in the fixed point; it is in tertiary symmetrical positions a double oblique cone whose summit lies at the fixed point. From this first property this important consequence follows, that in every plane inclined before the eye, assuming that it be considered in a secondary position, as is ordinarily the case, *every straight line must appear simple, providing that one of its points strike the eye*. Experiments have, however, revealed that all the straight lines lying in the normal surface, and none but such lines, appear perpendicular to the meridian plane, even in tertiary positions, where their real direction is quite different. If, for example, we look at a star formed of threads, whose rays lie in one plane, and fix our eyes upon its middle point, it will appear plane only in secondary positions, and curved in tertiary positions, and its rays then are deviated from the plane surface apparently in a direction opposed to that of the normal surface; the star only appears lying in a plane, in tertiary positions, providing an artificial curvature corresponding to the normal surface be given to it. Other researches show that every luminous point, whose distance cannot be determined by other methods, is projected in the line of direction into the normal surface. This surface appears therefore to be familiar to our eyes, and very probably it plays a very important part in stereoscopic vision, for the position of every part which does not lie within it is determined in accordance with it.

Rivalry of the Fields of Vision. Nature of Identity.

If there fall upon the two eyes, and upon corresponding retinal points, the images of objects which differ in outline, brightness, or colour, the one image or the other alternately occupies the common field of vision. Only such objects as can easily be fused into one whole give a compound, though indefinite, image. Combinations of shades (as grey, when black and white are presented to the two eyes) and of colours do not occur in some persons, whilst others perceive them at once, with the sensation of lustre. Between the impressions of the two eyes, phenomena of simultaneous and successive contrast are perceived, as if the excited retinal elements belonged to the same eye.

The facts here referred to, as well as others to be mentioned in relation to the stereoscope, teach us, that even in binocular vision the excitations of the two eyes remain distinct; it is therefore impossible that identity should depend upon the excitation of a common nerve-cell by two corresponding optic-nerve fibres. A more probable and very different explanation is this—that the impressions made upon *identical* spots of the retina are only fused by comparison with the objects contemplated in space, as the result of a psychical act; this fusion being effected empirically through the experience that, in the normal use of the eyes, the two impressions always spring from one object. This surmise explains alike the deviation from the strict law of identity which occurs in stereoscopic vision, as well as the convergence of the vertical lines of separation, which can be referred to the indefiniteness of the ground as a principal object; besides, in persons who squint, there is established a correspondence of retinal points which differs from that of persons whose vision is normal.

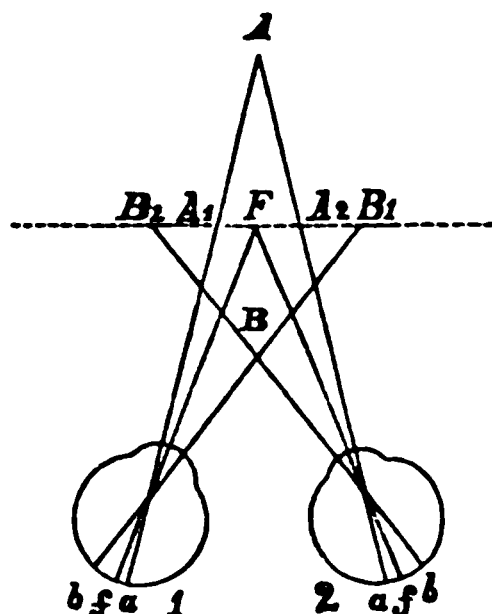
The question of the arrangement of the fibres of the optic nerve in the *chiasma* is of little importance in helping us to decide this question. Most authorities suppose that in man there occurs a partial decussation, so that the two right halves of the retina send their fibres into the right, and the two left halves into the left optic tract. It is only by such a supposition that we can account for the occurrence, as a result of paralysis of one optic tract, of that variety of *hemipia*, in which there occurs blindness of two corresponding halves of the retina, and consequently an obliteration of one half of the field of vision.

Animals occur in which there is an undoubted hemi-decussation of the optic tracts: such, for instance, is the case in the dog, in which animal, extirpation of one eyeball leads to a thinning of both optic tracts. On the other hand, animals occur in which the decussation is total: such are the osseous fishes, in which one optic nerve passes over the other, without any communication. Lastly, cases have been observed in man in which no decussation of the optic tracts has been observed, and in which vision has been normal. Further, as decussations which take place outside the brain might be partly or entirely compensated for within the brain, the question loses much of its importance in reference to the physiology of *identity*.

Double Images.

Objects, of which the images fall upon non-identical spots of the two retinae, must appear double. Yet this only occurs in a marked manner when the want of coincidence is great, and especially when it affects the regions in the

FIG. 58.



centre of the retina, as in cases of strabismus. In strabismus the visual axes of the two eyes intersect, so that the image of a point looked at falls upon two widely incongruous regions of the two retinae (which regions, however, occasionally become 'identical'). Two kinds of *diplopia*, or double vision, are found to occur, homonymous and *crossed*, according as the visual axes intersect in front of or behind the fixed point F (fig. 58).

It is evident that the points A and B, whose images fall upon symmetrical, and therefore non-identical halves of the retina, appear double, in the case of A appearing upon the same side of the retina, in the case of B upon the opposite side.

If we have in general only the consciousness of simple images, and fail to see any perturbations in the field of vision, it is because the following circumstances are probably in operation.

1. Objects which furnish images which fall on the centre of the retina (*fovea centralis* and *macula lutea*) appear simple under almost any circumstances, because the terminal points of the visual axes are corresponding points, and these axes, if prolonged, intersect at one point. Now as this is the seat of the most acute vision, and as the attention is almost constantly fixed upon it, the influence of the light falling upon it preponderates over the influence proceeding from the whole of the rest of the field of vision.

2. Objects which appear simple (which lie in the horopter) can impress consciousness with greatest intensity, seeing that they excite with double energy the same part of the nerve centres.

3. The eyes are always accommodated for those objects for which their axes are suited, so that they appear more sharply defined than those which are placed in front of or behind the point of intersection of the axes, and which are therefore not situated in the horopter.

This relation between the movements of the eyes and accommodation is brought about at first by the will, afterwards with the co-operation of a nervous mechanism (Czermak); in fact, the slightest movement of rotation of the eye is accompanied by a change in its accommodation, *e.g.* when the eye is rotated inwards it is accommodated for near objects.

4. Consciousness fuses, under certain circumstances, images of points which do not really correspond (see under Stereoscopy).

Co-operation of the two Eyes in Vision.

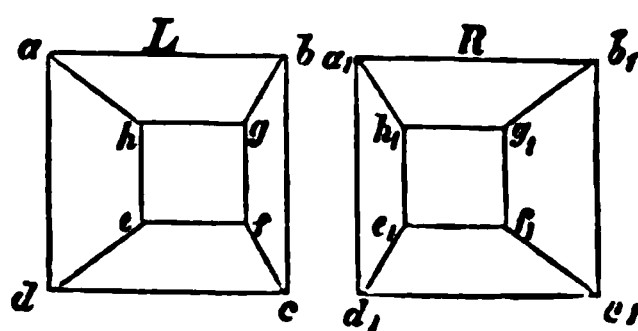
The most obvious advantage of vision with two eyes is, that portions of one retina which are incapable of discharging their function, *e.g.* by disease (*v. Graefe*), or portions of the retina which through opacities in the refracting media cannot receive images, are compensated for by corresponding points in the other retina. It is in consequence of this function of double vision that the mutual replacement of the gap in the field of vision due to the blind spot is filled up, for the corresponding points to the blind spots are parts of the retina which are sensitive to light (the blind spots are situated in retinal quadrants of different names, but symmetrical).

Stereoscopic Vision.

Stereoscopic vision, the perception of the third dimension occupied by bodies in space, depends upon the circumstance, that the two images of a material object or of a surface, which do not coincide with the horopter, can never be completely united (according to the theory of corresponding points) so as to furnish one single visual impression. As the two eyes contemplate the object from two separate points of view, two separate perspective images fall upon the two retinae. Now only exactly corresponding retinal images can uniformly fall upon corresponding points; when the eyes remain immovable only one part of a body can therefore appear single, the rest appearing double.

If, *e.g.*, L and R (fig. 59) are the two perspective retinal images

FIG. 59.

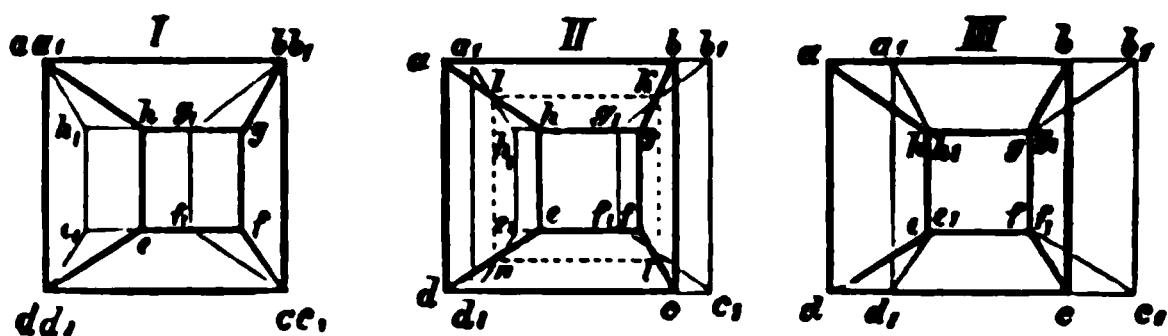


of a truncated pyramid, the summit of which is directed towards the eyes which contemplate it, it is seen that either the images of the surfaces of the base, viz. $a b c d$ and $a_1 b_1 c_1 d_1$, or the images of the truncated surface $e f g h$ and $e_1 f_1 g_1 h_1$, can alone fall upon corresponding points of the retina; in the first case, the smaller (truncated) surface appears double, in the second, the larger. Nevertheless, the two images are fused into one, and convey the impression of a single body occupying three dimensions. A simple explanation of this phenomenon would appear to be the following (*Brücke*): the two eyes are continually in a state of motion; their position of convergence varies so far from one side to the other,

that, one after the other, the images of all sections of the pyramids fall upon corresponding points of the retinae.

In fig. 60, three of the fusion-impressions which occur in two series of movements have been selected for examination. In the first the images of the basal-surfaces, and in the third those of the truncated surface, fall upon corresponding points; the image of a section of the pyramid situated between the two first ($i k l n$), and placed in the centre of the two first, is seen simply by the eyes. As now, in order that the impression exhibited by fig. 60, III., shall be perceived, the eyes must converge more strongly than for the perception of I.; and as the convergence of the eyes affords a means of determining the distance of objects from them (see below), the conclusion is arrived at by consciousness, that the surfaces $e f g h$, $i k l n$, and $a b c d$, lie one behind the other, and

FIG. 60.



the conception of a material object is arrived at, through the combination of all the rapidly succeeding impressions.

But the fact that the exceedingly short space of time during which an electric spark lasts suffices to fuse two simple stereoscopic images into one material impression, appears to afford an argument in opposition to the explanation above given, for in the moment of time during which the spark lasts no movements of the eyeball could take place.

This observation compels us to modify somewhat the theory of binocular vision. The identity of two corresponding retinal points is, namely, not to be taken as absolute, presumably does not depend upon a direct anatomical communication, but is *something which is acquired*.

Corresponding points are therefore such points as furnish images which, as experience teaches, are habitually combined or fused. But as it appears necessary to effect these combinations in order to obtain correct impressions of objects, we get into the habit of fusing also the images of two not perfectly corresponding points which under ordinary circumstances we should perceive as double. It can easily be demonstrated that simultaneous images, which fall upon corresponding points, are not united, although it is true that they do not form second images. When the mind must unite images which do not fall upon corresponding points, the process must be associated with the conception that the corresponding

points in the object occupy the situation for which the eye would have to be arranged, in order that the images should coincide.

We cannot here enter into an examination of the numerous theories which have been advanced in explanation of the above-mentioned facts. Moreover, Brücke's explanation of the stereoscopic fusion is not entirely refuted by the experiment of instantaneous illumination which was previously adduced, as, for the vision of complicated objects, such a movement of the eye from side to side is, at any rate, very useful. For the vision of such objects momentary illumination does not suffice.

Stereoscopic vision can be artificially imitated by placing before each eye the drawing of a body executed from its own point of view; such drawings are shown in fig. 59. The eyes in this case bring either successively or at the same moment the different parts of the drawing over corresponding points, and so the impression of the shape of body is produced. This is the basis of the stereoscope. Without further apparatus the images *R* and *L*, which lie side by side, may combine, if we direct each of the two optic axes to the corresponding image (fig. 61). But inasmuch as few persons can control their eyes for a sufficient length of time, in order to fix two separate points on a surface, instead of allowing as usual the axes to intersect at the surface which is looked at, arrangements are provided whereby this exertion is dispensed with, so that with an ordinary position of the eyes images are thrown upon corresponding points. The two best known stereoscopes are those of Wheatstone (fig. 62) and Brewster (fig. 63), which are explained by the annexed figures.

In the first (Wheatstone's) stereoscope the images are super-

FIG. 61.

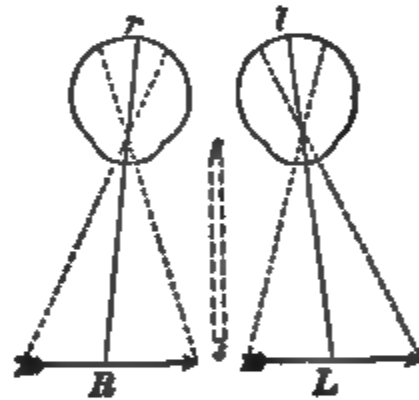


FIG. 62.

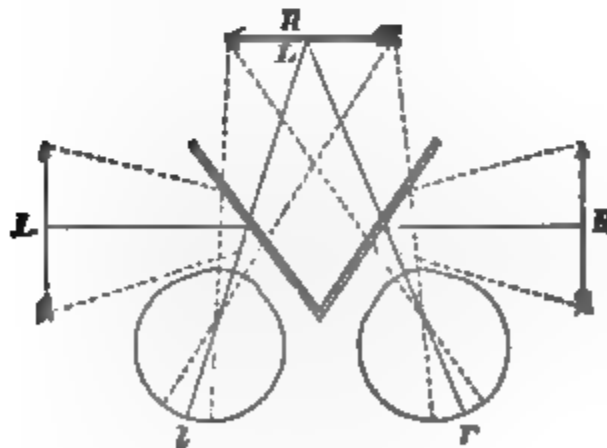
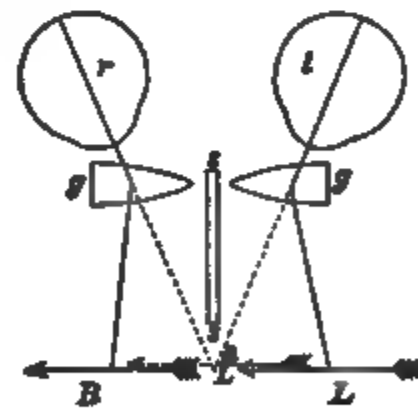


FIG. 63.



posed by two converging mirrors, in the second (Brewster's) by two prismatic glasses *g g* (halves of lenses) upon a place *R*, to which the optic axes are directed.

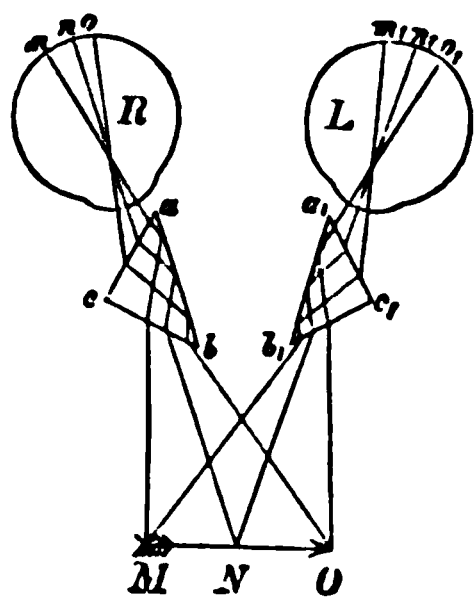
If two perfectly similar drawings are placed in the stereoscope, they naturally furnish a single image. If they are, however, ever so little different, the difference even being limited to the situation of certain parts, the eyes are compelled to make movements in order to combine these parts, and they appear, from what was previously stated, as removed from the surface, being either in front or behind it. Hence the stereoscope may be employed in order to distinguish between two similar objects which differ only in small and limited points, as, for example, between a real and a forged bank-note, as between two (different) impressions from the same mould, &c. (Dove).

If the relative positions of the stereoscopic image of a body be changed, for example, those seen in fig. 59, so that the one intended for the right eye is brought before the left, or conversely, the body appears hollow, and as if seen from within, the smaller surface, $e f g h$, appearing to be placed behind the larger. Actually the perspective views obtained by both eyes from a hollow pyramid, seen from the interior, only differ from those which are obtained on looking at a massive pyramid from the outside, in the fact that in the first case the right eye obtains the view which in the second case reaches the left eye.

On looking at an object from the outside, the right eye catches more of the right side of the object than of the left (the surface $b_1 c_1 f_1 g_1$ (fig. 59) is therefore larger than $a_1 d_1 e_1 h_1$); on looking into a hollow body matters are reversed (the right eye then occupies the point of view L , and $b c f g$ is smaller than $a d e h$). The fallacious impression obtained in such a manner by exchanging two stereoscopic images is designated 'pseudoscopic.'

The pseudoscope, fig. 64, is an apparatus by which the two eyes which are contemplating an object are subjected to a pseudo-

FIG. 64.



scopic influence; each eye receives, namely, by reflexion from the hypotenusal surfaces of a rectangular prism, the impression which belongs to it, reversed, so that one eye receives the form which properly pertains to the other. The body thus appears hollow and as if seen from the inside, when, in reality, its external surface is directed towards the eye, and conversely. The apparatus, as may readily be understood, can only be employed in looking at bodies which are symmetrically formed.

Very distant objects, *e.g.* those parts of a landscape which lie near the horizon, appear usually as if they were extended upon a surface, as in a picture, because the two eyes are situated too close to one another to obtain essentially different

views of objects in the distance. The *telestereoscope* of Helmholtz is an instrument which serves to magnify the distance between the points of view of the two eyes. It is a Wheatstone's stereoscope, the two images of which, L and R, are received by two mirrors turned towards the horizon and parallel to the internal mirrors; the two eyes thus obtain views as if they occupied the positions of the external mirrors, and the horizon appears, consequently, as if it had *stood-out* more; ordinarily the two internal mirrors are looked at through two telescopes.

When two stereoscopic representations of an object are coloured of different intensity (*e.g.* one being black, another white, or of a different colour)—or if two surfaces possessing different depths of the same colour, or coloured differently, be brought before the eye, the object or the surface appears to *shine*. The most probable explanation of this phenomenon is the following:—A surface which is looked at with one eye appears shining, when it reflects the light very uniformly; even absolutely plane or absolutely planely curved surfaces (if presenting no unevenness) therefore appear *shining*.

If this same surface be examined with the two eyes, it appears to each as possessing a different brilliancy and a different depth of tint, because the reflected light falls into the two eyes at a different angle. If now, conversely, the two eyes receive two impressions which when seen alone are dull, but if they are of different depth, consciousness pictures a regularly reflecting (which consequently illuminates the two eyes differently) and brilliant surface (Helmholtz). The two stereoscopic images of a smooth ball, which exhibit the reflexion of light at different places, give rise in the same way to the impression of a shining ball.

It is not so easy to explain the cause of the brilliancy of colours. The simplest explanation appears to be the following: besides arising by simple regular reflexion, certain sorts of brilliancy are generated by reflexion from multiple surfaces placed one behind the other, even when these surfaces are dull. Thus, for example, *metallic lustre* depends upon the fact that a slightly transparent metal not only reflects light from its surface, but also from its deeper layers (Brücke). As now for two different colours at an equal distance, a somewhat different accommodation of the eye is requisite, it appears as if one colour lay a little behind the other, and so the body exhibits lustre (Dove). Moreover, many persons fail to observe the binocular combination of colours, both colours not uniting to form one image, but they either appear alternately or are seen side by side in the field of view ('Rivalry of the Fields of Vision').

Estimation of Magnitude and Distance of Objects.

A third useful purpose subserved by binocular vision is the aid which it affords in the determination of the magnitude and distance

of external objects. The starting-point for the determination of magnitude is the size of the retinal image. The greater the latter, the greater, *cæteris paribus*, does the object appear. As, however, the magnitude of the retinal image, or what is the same, the magnitude of the visual angle, does not depend merely upon the magnitude, but also upon the distance of the object from the eye (as the visual angle is inversely proportional to the distance), the determination of the magnitude of objects is associated with a determination of their distance. For the latter, the eye by itself possesses a method of estimation, in the effort to accommodate, the magnitude and direction of the effort being appreciated by the muscular sensation in the muscle concerned. In vision with two eyes there is added the important help afforded by the muscular sense of the muscles which move the eyeball, and which inform us to what degree the optic axes have converged.

An object of apparently equal magnitude appears the nearer, 1, the greater the retinal image which it furnishes; 2, the stronger the positive accommodation; 3, the stronger the convergence of the optic axes. Further helps to the determination of distance are, the intensity of the light, which in general decreases with the distance. Further, the displacement of the object in reference to others seen at the same time, which occurs either when the object itself moves, or when the other objects move, or when the organ of sight changes its place in consequence of movements of the head or of the whole body.

The most direct proofs that the above are the three principal means of estimating the distance or size of objects are the following:

1. The influence of the retinal image scarcely requires proof; such a proof is, however, that in defective accommodation (in the circles of diffusion) an object seen appears larger than if the accommodation be perfect and the object sharply defined.

2. The influence of the sensation produced by accommodation is most apparent from the fact that a secondary image, however produced, changes in apparent magnitude when the accommodation changes; and further, that if red and blue fields occupy the same plane, the first appear nearer than the second (Brücke).

3. The influence of the convergence of the axes is proved in a striking manner by the so-called 'carpet-phenomenon.' If whilst one is looking at any regular pattern (as a carpet) the eye be fixed upon a point lying in front of or behind it, the pattern soon appears to advance in the plane of the point of convergence of the visual axes, and appears, consequently, near or more distant, and in the same manner smaller or larger.

The explanation is easy. Under these circumstances an irregular pattern would appear double; even a regular pattern will appear double; but as in the two images situated one over the other, equal parts of the pattern almost exactly cover one

another, the deception originates that both images with their corresponding parts fall upon corresponding points, and therefore the object lies at the distance of the point of intersection of the visual axes (H. Meyer). Just as the images of the centres of the two retinæ are transferred to the point of intersection of the visual axes, so the remaining images are transferred to the surfaces, in which the identical meridians intersect, *i.e.* to the normal surface.

The Organs which protect the Eye.

1. The eye, which is protected nearly on all sides by the osseous orbit in which it is placed, can also be shut off anteriorly by the closure of the cartilaginous eyelids. The closure is effected by the contraction of the *orbicularis palpebrarum* muscle, which receives its nervous supply from the facial nerve, and in so far as the upper eyelid is concerned, it is brought about to a certain extent by the mere action of its weight (gravity). The lower eyelid is opened by the action of gravity, the upper by the contraction of the levator palpebræ superioris, which derives its nervous supply from the third (oculomotor) nerve, whilst both are influenced by *retractor* involuntary muscular fibres which are under the influence of the sympathetic (H. Müller, Sappey). Movements of opening and of closure are frequently and alternately occurring (blinking, winking).

The closure of the eyelids occurs, 1, voluntarily; 2, involuntarily and automatically, in sleep; 3, by reflex action, when the eyeball is touched or the eyelashes which serve as touch-hairs, or when the optic nerve is excited by intense light. The narrowing of the space between the eyelids and the shade thrown by the eyelashes co-operates with the contraction of the pupil in protecting the eye when the light is intense.

The retractors of Müller are situated in the posterior surface of the eyelids perpendicular to the opening between the lids. Another smooth muscle bridges over the inferior orbital fissure, and by its contraction somewhat diminishes the capacity of the orbit, so that the eyeball somewhat projects. Both muscles exist in a state of tonic contraction. When the sympathetic is cut cross in the neck the space between the lids narrows and the eyeball is somewhat retracted (H. Müller).

2. The anterior surface of the eye is continually bathed in lachrymal fluid, and by it maintained in a state of cleanliness and preserved from dessication. The tears reach it through the fine excretory ducts of the glands situated in the upper and external region of the conjunctival sac. (The conjunctival sac is, as is well known, a mucous sac, which by its free border is attached along the edge of the lids, and which covers a part of the eyeball; it covers the posterior surface of the eyelids, then is reflected over the eyeball, of which it covers the anterior third. The eyelids being closely applied to the eyeball, the conjunctival sac possesses

only a capillary lumen. It only widens near the line of contact of the closed lids, where it forms a shallow three-sided canal, as the more slight curvature of the lids does not here permit of their clasping the eyeball). The tears are sucked into the capillary conjunctival space by capillary attraction, and are pressed towards the inner angle of the eye. This movement is aided by the closure of the lids, which presses them towards the inner angle of the eyes (inner canthus), which is the point of attachment of the orbicularis palpebrarum.

The overflow of tears over the fine edge of the lids is prevented, when the secretion is not exceedingly great (as in crying), by the fatty secretion of the *meibomian glands*. At the inner angle of the eye the tears accumulate into what may be called a little tear-lake ('Thränensee'), where commence the two capillary rigid lachrymal canals with their openings, the 'puncta lachrymalia.' The nasal duct, into which the ducts lead, and which is protected below in the nasal cavity by a valve opening downwards, dilates superiorly at the time when the eyelids are closed (because its posterior wall is connected with the bone, and its anterior with the anterior palpebral ligament which stretches when the lids are closed); by these arrangements it sucks the tears from the little tear-lake. The same effect is produced by the contraction of Horner's muscle, which also enlarges the lachrymal sac.

The closure of the lids might also, when the lids are completely closed, press the tears into the sac. This has actually been recorded to occur by some (Rose, Stellwag, v. Carion). Experiments with coloured fluids, which have been instituted to decide this question, have not furnished concordant results (Stellwag, Arlt).

3. The eyebrows are supposed to protect the eye from the sweat which may flow from the forehead.

Appendix.—The faceted eyes of insects and crustacea are composed of conical segments arranged as the radii of a ball: each of these segments consists of a dioptric apparatus which acts as a convex lens, and of internal nervous structures which are in connection with the terminal ends of the optic nerve in the centre of the ball. Each of these radiating segments, which by pigment and by total reflection (like the rods of the retina) are optically distinct one from the other, most probably only allows such light to be perceived as falls in the direction of its axis, so that the creature possesses, especially for near objects, as many fields of view as there are segments. The adjustment of an optic nerve-element to a particular direction is effected here also, as in the eyes of vertebrata, by other means. In the latter, for instance, the complex dioptric apparatus only allows such light to reach each individual retinal element as follows a particular direction (viz. that of the corresponding visual ray); in the eye of insects, on the other hand, each retinal element has a telescope arranged for one particular direction.

II. THE ORGAN OF HEARING.

Schema of the Organ of Hearing.

The terminal organs of the auditory nerve are spread out like those of the optic nerve on membranous surfaces, which have, however, an irregular form (*ampullæ, saccules of the vestibule, and membranous portion of the lamina spiralis*). The sonorous vibrations capable of exciting the auditory nerve are transmitted to these terminal organs by a system of easily vibrating bodies in contact with each other, the first of which, situated most externally, vibrates in unison with the sounding body; the vibrations of the sonorous body are transmitted to it directly or indirectly: in the latter case through an intermediate body, such as air or water.

There are two such systems, and these have one part in common,—that adjacent to the end organs, viz. the fluid contents of the labyrinth in which the terminal organs are bathed. The labyrinth-fluid can be thrown into vibrations in two ways: 1, by the surrounding bones,—the petrous portion of temporal and all the other cranial bones. This mode of transmission comes into play when the sonorous (solid) body is either in immediate contact with the skull, or is connected with it by a chain of solid or fluid bodies, or when the medium immediately surrounding the head is not gaseous, as, for instance, when the surrounding body is in contact with the teeth, or when the head is immersed in water; 2, by the *membrane of the fenestra ovalis*, which separates the labyrinth-fluid from the air-containing tympanic cavity. This membrane is thrown into vibrations by the following chain of bodies (beginning from the fenestra ovalis): *stapes, incus, malleus, membrana tympani*, the *air and walls of the external meatus and auricle*. This system serves for the perception of those sonorous vibrations which are transmitted to the ear by the air: it is therefore the common form of conduction in man, and is found absent in aquatic animals.

Of the two systems just enumerated the latter alone requires further consideration, for the first plays in the case of man only a very secondary part.

Mechanism of the Sound-Conducting Apparatus.

It is chiefly at the surface of the *membrana tympani*, but also at the walls of the auricle and external meatus, that the transference of the sonorous vibrations from air to solids takes place. The vibrations communicated to the auricle and external meatus are for

only a capillary lumen. It only widens near the line of contact of the closed lids, where it forms a shallow three-sided canal, as the more slight curvature of the lids does not here permit of their clasping the eyeball). The tears are sucked into the capillary conjunctival space by capillary attraction, and are pressed towards the inner angle of the eye. This movement is aided by the closure of the lids, which presses them towards the inner angle of the eyes (inner canthus), which is the point of attachment of the orbicularis palpebrarum.

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The terminal organs of the auditory nerve are spread out like those of the optic nerve on membranous surfaces, which have, however, an irregular form (*ampullæ, saccules of the vestibule, and membranous portion of the lamina spiralis*). The sonorous vibrations capable of exciting the auditory nerve are transmitted to these terminal organs by a system of easily vibrating bodies in contact with each other, the first of which, situated most externally, vibrates in unison with the sounding body; the vibrations of the sonorous body are transmitted to it directly or indirectly: in the latter case through an intermediate body, such as air or water.

There are two such systems, and these have one part in common,—that adjacent to the end organs, viz. the fluid contents of the labyrinth in which the terminal organs are bathed. The labyrinth-fluid can be thrown into vibrations in two ways: 1, by the surrounding bones,—the petrous portion of temporal and all the other cranial bones. This mode of transmission comes into play when the sonorous (solid) body is either in immediate contact with the skull, or is connected with it by a chain of solid or fluid bodies, or when the medium immediately surrounding the head is not gaseous, as, for instance, when the surrounding body is in contact with the teeth, or when the head is immersed in water; 2, by the *membrane of the fenestra ovalis*, which separates the labyrinth-fluid from the air-containing tympanic cavity. This membrane is thrown into vibrations by the following chain of bodies (beginning from the fenestra ovalis): *stapes, incus, malleus, membrana tympani*, the *air and walls of the external meatus and auricle*. This system serves for the perception of those sonorous vibrations which are transmitted to the ear by the air: it is therefore the common form of conduction in man, and is found absent in aquatic animals.

Of the two systems just enumerated the latter alone requires further consideration, for the first plays in the case of man only a very secondary part.

Mechanism of the Sound-Conducting Apparatus.

It is chiefly at the surface of the *membrana tympani*, but also at the walls of the auricle and external meatus, that the transference of the sonorous vibrations from air to solids takes place. The vibrations communicated to the auricle and external meatus are for

only a capillary lumen. It only widens near the line of contact of the closed lids, where it forms a shallow three-sided canal, as the more slight curvature of the lids does not here permit of their clasping the eyeball). The tears are sucked into the capillary conjunctival space by capillary attraction, and are pressed towards the inner angle of the eye. This movement is aided by the closure of the lids, which presses them towards the inner angle of the eyes (inner canthus), which is the point of attachment of the orbicularis palpebrarum.

The overflow of tears over the fine edge of the lids is prevented, when the secretion is not exceedingly great (as in crying), by the fatty secretion of the *meibomian glands*. At the inner angle of the eye the tears accumulate into what may be called a little tear-lake ('*Thränensee*'), where commence the two capillary rigid lachrymal canals with their openings, the '*puncta lachrymalia*.' The nasal duct, into which the ducts lead, and which is protected below in the nasal cavity by a valve opening downwards, dilates superiorly at the time when the eyelids are closed (because its posterior wall is connected with the bone, and its anterior with the anterior palpebral ligament which stretches when the lids are closed); by these arrangements it sucks the tears from the little tear-lake. The same effect is produced by the contraction of Horner's muscle, which also enlarges the lachrymal sac.

The closure of the lids might also, when the lids are completely closed, press the tears into the sac. This has actually been recorded to occur by some (Rose, Stellwag, v. Carion). Experiments with coloured fluids, which have been instituted to decide this question, have not furnished concordant results (Stellwag, Arlt).

3. The eyebrows are supposed to protect the eye from the sweat which may flow from the forehead.

Appendix.—The faceted eyes of insects and crustacea are composed of conical segments arranged as the radii of a ball: each of these segments consists of a dioptric apparatus which acts as a convex lens, and of internal nervous structures which are in connection with the terminal ends of the optic nerve in the centre of the ball. Each of these radiating segments, which by pigment and by total reflection (like the rods of the retina) are optically distinct one from the other, most probably only allows such light to be perceived as falls in the direction of its axis, so that the creature possesses, especially for near objects, as many fields of view as there are segments. The adjustment of an optic nerve-element to a particular direction is effected here also, as in the eyes of vertebrata, by other means. In the latter, for instance, the complex dioptric apparatus only allows such light to reach each individual retinal element as follows a particular direction (viz. that of the corresponding visual ray); in the eye of insects, on the other hand, each retinal element has a telescope arranged for one particular direction.

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the most part conducted further to the membrana tympani along its ring of attachment; a portion of these reaches the labyrinth through direct conduction by the bones, together with all those vibrations which are imparted to the head by the air. Moreover, the walls of the external meatus, and possibly also of the auricle, reflect the sonorous waves on to the membrana tympani.

The particles of air vibrate longitudinally, i.e. in the direction of the propagation of the sound; hence arise alternate layers of rarefaction and condensation in planes perpendicular to the direction of vibration. The distance of two contiguous layers in the same plane of vibration constitutes a *wave-length*—if by l we designate the wave-length, by c the rate of propagation of the wave, by t the duration of a complete oscillation, by n the number of vibrations in the second, then

$$l = ct = \frac{c}{n}$$

There is no form of solid body more adapted for the reception and further transmission of vertically or obliquely impinging air-vibrations than that of a stretched membrane or of rigid, elastic, thin plates. To the latter description the cartilaginous auricle answers, whilst the membrana tympani is of the first-described form. In both cases the body is so thin that the waves of condensation and rarefaction of the air which fall on it are capable of setting *its total mass* in vibration, in the direction of its transverse diameter (transverse vibrations); otherwise the different layers of molecules would vibrate successively, and thus give rise to condensation and rarefaction waves in the body itself (longitudinal vibrations); in the first case, where the elasticity has only to be overcome, the resistance is much less and the elongation of the vibrations therefore much greater, than in the latter case, where the greater resistance is opposed to the mutual separation of the molecules. Such bodies, however, are also capable of longitudinal vibrations, when vibrations are communicated to them from the border, as e.g. the vibrations transmitted to the membrana tympani by the external meatus.

The *reflexion* of sound by the walls of the external meatus requires no further elucidation, for all vibrations which fall on the walls of a cylindrical tube must reach, after being once or oftener reflected, the surface which closes the tube (in the case of the ear, the membrana tympani, which is placed obliquely to the axis of the tube, passing from below upwards, and outwards).

Reflexion of sound waves from the surfaces and promontories of the auricles on to the orifice of the auditory meatus may very well be thought possible, especially as the auricle, both *in toto* as well as in its separate parts, is movable by means of muscles (which, however, owing to non-use, are often but ill developed). Experiments, however, in which the whole auricle, with the exception of the meatus (which was prolonged by means of a tube inserted into it) was filled up with a soft material, showed no perceptible diminution of the hearing, from which the function of the auricle as a reflector of sound would seem improbable (Harless); others, however, have obtained opposite results (Schneider). The absence of the auricle has not been known to cause diminution of hearing. Artificial reflectors of considerable power (for people affected with difficulty of hearing) are *ear trumpets*, which may be considered to be cylindrical prolongations of the meatus, with a funnel-shaped external termination. The *stethoscope* may be considered as a similar prolongation of the meatus, the other end of which is in contact with the sonorous body; its action, however, depends, to a great extent, on the conduction of sound along its walls.

The membrana tympani has the form of a flattened cone or funnel, the meridians of which, owing to the tension of the cir-

cular fibres, are not straight, but somewhat curved, with the convexity outwards, the manubrium of the malleus being inserted between the lamellæ of the membrane in a radial direction, passing from above downwards, and terminating a little below the centre of the membrana.

The malleus is supported by a ligamentous mass which is stretched from before backwards through the tympanic cavity, forming at the same time the axis of rotation (axial band, Helmholtz); this band consists of two ligaments, inserted into the neck of the malleus, an *anterior ligament*, attached to the spina tympanica anterior, and a *posterior ligament*, which is only a prolongation of the anterior. The movements of the membrana tympani being communicated to the manubrium of the malleus, the latter, and with it the incus, rotate round the axis just described; the incus is chiefly supported by the malleus, but it is so connected by its short process to the posterior wall of the tympanic cavity, that it slightly modifies the movements of the malleus (so that both might be considered as forming one complex lever), and allows the umbilicus of the tympanic membrane to move only in a direction vertical to the plane of the membrane. The long process of the incus, which articulates with the stapes, curves round a little inwards from the manubrium of the malleus, remaining throughout parallel to it. The articulation between malleus and incus is saddle-shaped, the body of the incus surrounding the convexo-concave articular surface found on the neck of the malleus. The articular surfaces are provided with a kind of *check tooth*, so that only the rotations inwards of the malleus are exactly communicated to the incus, but not the rotations outwards; from this it follows that the stapes cannot be torn away from the fenestra ovalis by such outward movements of the tympanic membrane, while the tension of the latter membrane provides against the forcing in of the stapes (Helmholtz).

The tendon of the tensor tympani, which, after passing over its pulley and running at right angles to the manubrium, inserts itself into the point of rotation of the malleus, draws with every contraction of its muscle the manubrium still more inwards, and thus brings about a still further tension of the tympanic membrane. The contraction (dependent on the fifth nerve) can be produced by some persons voluntarily (J. Müller); it is observed in all persons as a co-ordinate movement in connection with the forcible contraction of the muscles of mastication (Fick). Opinion is as yet divided as to whether the contraction is purely a voluntary one or a reflex action (to damp strong impressions of sounds), dependent on the auditory nerve or the sensory nerves of the external meatus. As soon as the contraction of the muscle ceases, the manubrium and, with it, the tympanic membrane, return to their position of equilibrium by help of the elasticity of the membrane,

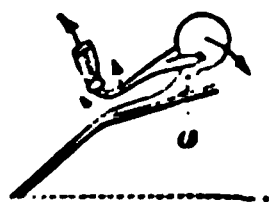
and the arrangement of the ligamentous appendages of the malleus and the connection of the different joints of the ossicles.

The small *stapedius* muscle which, passing from behind and at right angles to, inserts itself into the neck of the stapes, and which derives its nervous supply from the facial nerve, exerts traction from behind on the articulation between the incus and stapes. The consequences of this action are not apparent; many ascribe to it a movement outwards of the chain of ossicles, therefore an action tending to release the *membrana tympani*, and therefore antagonistic to that of the *tensor tympani*.

Many persons can produce at will a crackling noise in the ear, which formerly was thought to be connected with the contraction of the *tensor tympani* (muscular sound or sudden stretching of the tympanic membrane). This assumption is contradicted by the fact that the sound is not accompanied by a drawing inward of the *membrana tympani* (this is ascertained by inserting a manometer into the meatus, Politzer, Löwenberg). This sound is now thought to be produced by the sudden opening (by the *tensor palati*) of the Eustachian tube, which, according to some (Toynbee, Politzer, Moos) is considered to be quite closed while at rest.

The chain of ear ossicles serves the purpose of transmitting the vibrations of the tympanic membrane to the membrane of the fenestra ovalis. In birds, and in the scaly amphibia, they are represented by a single rod-like ossicle (*columella*) only. In man the two opposed membranes are not connected by a single rod, but by a compound lever composed of three bones, the axis of rotation of which is the malleo-incus axis (a , in fig. 65).

FIG. 65.



The arrows in the figure indicate how the membrane of the fenestra ovalis must always vibrate in the same sense as the *membrana tympani*. The impulses of the base of the stapes produce progressive waves in the labyrinth, *i.e.* the fluid contents of the labyrinth recede *in toto* with every impulse, thereby causing the yielding part in the wall of the labyrinth, the *fenestra rotunda*, to arch outwards towards the tympanic cavity. It is not possible to discover what parts of the labyrinth, and especially how the fluid contained in the semicircular canals, take part in the movements which are set up.

Inasmuch as the dimensions of the whole sound-conducting apparatus are very small in relation to the wave-lengths of the sounds which can be heard, we must surmise that all the constituent parts are at the same time in the same phase of vibration, and that the combination vibrates backward and forward (E. Weber, Helmholtz). The vibrating structures in the ear behave therefore in respect to sound as resonators. Artificial resonators are only thrown into vibration by such tones as correspond with their own proper tone. That the ear not only is affected equally well by different tones, but that it can follow every sound and every noise, is the most important fact in acoustics. Even if we

assume that in the ear a decomposition of every sound into its constituents is brought about by a series of resonators, we must recognize that, before such a decomposition can take place, the conduction of sound in all its details must occur; it is obvious, then, that the outer sound-conducting parts of the organ of hearing, especially the *membrana tympani*, must possess other properties than those which pertain to ordinary resonators, *e.g.* to stretched membranes. Smallness of mass and great resistance appear to be the principal causes which diminish the influence of the proper tone, exactly as they diminish the influence of inertia-waves in manometers, &c.

Another circumstance tending to diminish the disturbance from the proper tone is this,—that waves of very small amplitude suffice to stimulate the extremely sensitive auditory nerves; while with small amplitude of wave the influence of the proper tone is at a minimum. Indeed, appliances exist in the ear for diminishing amplitude with a corresponding gain in force. Thus a consideration of the outward curvature of its meridians shows that the conical tympanic membrane must receive all impulses in such a manner that they react upon its apex as if they had been received on the long arm of a lever, which moved the apex by means of its short arm. And of similar import is the circumstance that the manubrium of the malleus, reckoned from the axis of rotation, is one and a-half times as long as the long process of the incus (Helmholtz), a relationship in regard to which fig. 65 is incorrect.

In view of the small amplitude of wave needed to affect the auditory nerves, it is highly improbable that the articulations of the auditory ossicles have any special part to play, or that the membrane of the *fenestra rotunda* is pushed outwards at every vibration of the system. These arrangements seem rather designed to render the labyrinthine liquids independent of the variations in position of the tympanic membrane.

Hence we can understand how hearing is possible even in the absence of tympanic membrane and auditory ossicles, under which conditions the air acts as conductor, and the *fenestra ovalis* and *fenestra rotunda* both take up the vibrations. That the *fenestra rotunda* is capable of doing so is shown by the fact that it may actually be seen to vibrate in response to aerial waves of sound (though not to such as are conducted through bone) after the *fenestra ovalis* has been firmly closed (Weber—Liel).

Although the tympanic membrane follows exactly all sorts of vibrations, yet its proper tone, when opportunity offers, shows that it is not without its influence. Thus, an increase of tension of the membrane, which raises its proper tone, renders higher tones more distinctly audible, and thus a sort of accommodation for high tones becomes possible; but about the actual exercise of this accommodation little is certainly known. Moreover, a high tension of the tympanic membrane diminishes the intensity of the

vibrations, and hence exerts a damping influence (J. Müller). Such an exalted tension would be brought about by contraction of the tensor tympani muscle, while in all probability the stapedius muscle has the opposite effect of diminishing the tension. But, in addition, the position and tension of the tympanic membrane are closely dependent on the atmospheric pressure of the tympanic cavity, which again can be brought into dependence on that of the outer air through the Eustachian tube. This tube—a bony tunnel at the ear, but possessed of membranous and cartilaginous walls at its pharyngeal extremity—is regarded by most observers as constantly closed except during the act of swallowing, when it is momentarily opened. If from any cause it be kept permanently closed, the deviation of the pressure within the tympanum from the normal brings about a change in position of the membrane, and consequent deafness.

Such deviations may artificially be produced, in what is known as Valsalva's experiment, by first closing the oral and nasal openings and then making strong expiratory or inspiratory efforts.

In addition to an accommodation of the tympanic membrane for high tones by means of the tensor tympani muscle, an accommodation for low tones is said to be possible by means of the stapedius. The former occurs as an associated movement on closing the mouth, and the latter on firmly shutting the eyes (Lucae).

A cross-section of the Eustachian tube at the pharyngeal end has the form of a vertical slit which is bent outwards above. Within the angle of the bend, fibres of the tensor palati muscle are inserted into the outer wall of the tube, and, on contracting, draw it away from the inner wall, thus opening the tube. This occurs with every act of deglutition, and probably also of yawning. It should, however, be remarked that the mechanism of opening the Eustachian tube is still much debated. Thus some deny any participation of the tensor palati in the act, since during its occurrence the velum palati remains at rest (Yule) and accounts differ even about the usual state of the pharyngeal end of the tube. In short every possible condition has been suggested, from constant closure except at swallowing (Toynbee, Politzer, Moos, and others), to constant openness (Rüdinger, Lucae), and even constant openness *except* in the act of swallowing (Cleland, Lucae). It matters not that marked variations of atmospheric pressure, in a confined space, cause perceptible movements of the tympanic membranes (Mach and Kessel), for such would be the effect even if the Eustachian tube were patent, provided the opening were small enough (Lucae).

It is hardly probable that the Eustachian tube is a means of hearing one's own voice; for it may, as above stated, be closed for the greater part of the time, and the voice sounds abnormal in circumstances where the tube is undoubtedly open.

The closure of the Eustachian tube is of advantage for the powerful conduction of sound; as is also the communication of the tympanic chamber with the irregular cavities of the mastoid cells (Mach and Kessel).

Just as normally the vibrations of the air are transmitted to the vibrating parts of the organ of hearing by the membrana tympani, so the reverse happens when the organ of hearing is *primarily* (by conduction through bone, as, *e.g.* in the case of one's own voice) set in vibration; this mode of conduction diminishes the vibrations of the ear (Mach). By preventing the transmission of vibrations outwards (closing the meatus) the sound of one's own voice, conducted by the bones, is increased (Weber).

Excitation of the Terminal Organs of the Auditory Nerve.

The end-organs of the auditory nerve are distributed on the inner surface of the hollow structures which fill the greater part of the labyrinth. In man there are distinguished two sets of these structures: 1. The Utricle, with the membranous labyrinth of the semicircular canals almost filling their osseous counterpart; 2. The Sacculæ, with the *canalis cochlearis* of the cochlea. The latter cavity is formed by two membranes, the *membrana basilaris* and the *membrane of Reissner*, which proceed from the edge of the lamina spiralis and radiate outwards to two points of the periphery of the spiral cavity of the cochlea. The canal included between these membranes projects, at the base of the cochlea, into the vestibule, and is connected with the sacculæ by the fine *canalis reuniens* (Hensen).

Both sets of organs are lined with a continuous epithelium and filled by a viscid liquid, *endolymph*. The rest of the bony labyrinth—viz. the vestibule outside the utricle and sacculæ; the narrow space of the osseous semicircular canals outside the membranous canals; and lastly the spaces above and below the lamina spiralis and the *canalis cochlearis*, or, in other words, the *scala vestibuli* and the *scala tympani* leading to the *fenestra rotunda*—all these spaces are filled by a peculiar thin liquid, the *perilymph*. Of these liquids the endolymph may be likened to the vitreous body of the eye, and the perilymph to the aqueous humour.

The present state of knowledge as to the terminal organs of the auditory nerve may be stated as follows:—

1. *Nerve-Endings in the Ampullæ and Vestibular Sacs (Sacculæ and Utricle).*—In the *ampullæ* the nerve-endings are contained in a yellowish, semicircular, equatorial septum, which is a thickening of the membranous labyrinth (Scarpa, Steifensand, M. Schultze). Its structure, particularly in the skate, as investigated by M. Schultze, may be thus described. The simple epithelium of the ampullæ is raised on the septum of hard connective tissue, so as to form a thick cushion consisting of several layers, from which fine stiff bristles (the *auditory cirrhi*) project, of such length as almost to reach the opposite wall of the ampullæ. The nerves, which suddenly part with their medullary sheaths at the border of the connective tissue, are distributed in the epithelial mass, breaking up into naked axis-cylinders of extreme fineness.

The cells of the epithelial layer are of the following kinds:—

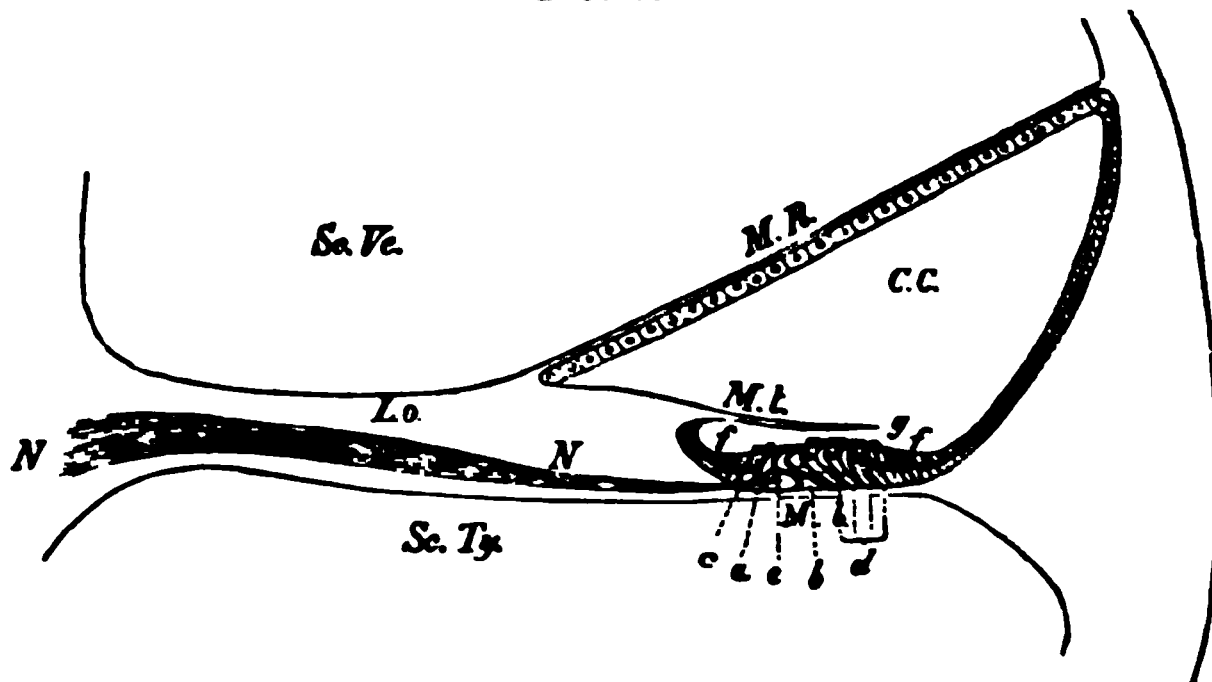
a. Several layers of cylindrical nucleated epithelial cells, of which the deepest (called '*Basal-cells*') are somewhat pyramidal and pointed. b. Spindle-shaped cells, each of which has two long fine processes, one of which is directed towards the surface where it seems to end, while the other, which is frequently varicose (these varicosities being, according to Schultze, artificial products), tends towards the base, its mode of termination being uncertain. These spindle-shaped cells, with their fibres, are nervous structures, and are supposed to constitute the ends of the fine axis-cylinders. c. Round or cylindrical cells in the superficial layer, each of which sends out one of the auditory cirrhi or hairs already referred to. According to some, these cirrhi spring out of the superficial processes of the nerve cells.

In the vestibular sac, as observed in fishes, the nerve-endings are in like manner contained in a crescentic septum, which, however, is less elevated. In this structure the same elements are found as in that of the ampullæ, with the exception of the cirrhi, the place of which is taken by the *otolith*. This is accurately applied to that part of the inner wall of the sacculus which bears the septum, for the reception of which it is grooved. The otolith consists of a hard or pasty mass of minute prisms of calcic carbonate in the form of arragonite, and, invested by a soft sheath, is suspended in the viscid fluid resembling vitreous humour (*endolymph*) which occupies the cavity (M. Schultze). Here and there short cirrhi are to be seen where the otolith is not applied to the surface.

In Mammalia, instead of a crest or ridge, there is found a shallow *Macula acustica*, covered with otolithic powder. According to more recent researches on mammals (Pritchard), the nervous epithelium of the ampullæ and sacculus contains two sorts of hair-cells, one sort provided with stouter cirrhi than the other. The cirrhi of both sorts protrude through a thick *cuticula* corresponding to the *membrana reticularis* of the cochlea. The sheaths of the otoliths appear to represent the *membrana tectoria* of the cochlea.

2. *Nerve-Endings in the Cochlea (Organ of Corti).*—The special canal which winds round the columella of the cochlea is divided into three channels, viz. the *Scala vestibuli* (Sc. Ve. fig. 66), the *Scala tympani* (Sc. Ty.), and the *duct of the Cochlea* (C.C.) which lies between them—by the bony part of the lamina spiralis

FIG. 66.



(*L.O.*), and by the two membranes which stretch across from this structure to the outer wall of the canal, namely, the *membrana basilaris* (*M. b.*) and the *membrane of Reissner* (*M.R.*) The fibres of the cochlear nerve, which are contained in the columella, spread out from it in the form of a fan, which winds spirally round it, entering the duct of the cochlea by the radiating canaliculi of the lamina ossea (*N.N.*), in order to reach the *organ of Corti*. This organ, according to the latest researches (Kölliker, Böttcher, Waldeyer and Gottstein, v. Winiwarter), has the following structure:—The epithelial lining of the duct of the cochlea assumes on the *membrana basilaris* a peculiar development. In every radial section, two hardish elastic pillars (*a* and *b*) are seen, which articulate with each other by their heads. These are called the '*arches or pillars of Corti*.' On the inner side of each internal pillar an '*internal hair-cell*' (*c*) is to be found, which is in connection with the nerve fibre. In like manner, on the outer side of the outer pillar, there are a number of '*external hair-cells*' (*d*). These (which in mammalia generally are three in number, but in the human cochlea four or five, while in birds and amphibia they are wanting) are also provided with nerve fibres (*e*). The heads of the pillars of Corti have each of them a process by which it contributes to the formation of a supporting net-

work (the *lamina reticularis*), the level of which coincides with that of the epithelial border (*lamina reticularis*, *f. f.*) In the rings of this beautiful network, the heads of the hair-cells fit in quincuncial arrangement. The whole organ of Corti is covered by a soft membrane (*M. t.*), which springs from the *lamina ossea*, and floats by its free edge (*g*) in the fluid of the cochlear duct. (The drawing is diagrammatic.)

As already remarked, the course of the sonorous waves cannot be tracked through the complicated labyrinth and the various media contained in it. The circumstance that part of the auditory nervous epithelium is provided with cirrhi projecting into oscillating endolymph, while another part is in contact with hard bodies suspended in the same medium, has been thought to favour the hypothesis that stimulation of the auditory nerve is brought about mechanically by the vibrations of the endolymph, as in the mechanical production of tetanus in ordinary nerve. This explanation must be received with caution, because, in the first place, cirrhi or cilia are not confined to the auditory organ, but are found in other organs of sense; and, in the second place, the intensity of the supposed labyrinthine stimuli is indefinitely small as compared with the intensity of the mechanical stimuli needed to affect other nerves. Hence it is necessary to assume for the auditory nerve a peculiar sensitiveness; which is practically confessing that we know as little about the stimulation of the auditory nerve by sound as of the optic nerve by light.

The peculiar function of individual parts of the labyrinth will be discussed below.

Characteristics of the Sensation of Hearing.

The excitation of the terminal organs of the auditory nerve by the vibrations of the liquid contents of the labyrinth, or any other excitation of the auditory nerve fibres, causes an auditory sensation. The 'amplitude' of the waves determines the *intensity* of the perception of sound, while the 'length' of the waves, or the number of the vibrations in a given time, determines the *pitch* of the tone heard.

As regards pitch, the range within which sounds can be distinguished is very considerable, and the limits are probably determined, not by the excitability of the auditory nerve, but by the vibratory capacity of the transmitting organs, *e.g.* of the tympanum.

The interval between the lowest tone audible (40 vibrations) and the highest (16,000 to 20,000) amounts to $8\frac{1}{2}$ or 9 octaves, whereas the interval between the limits of visibility of the red and violet rays reckoned in an analogous manner does not reach one octave.

The limits of audibility are often much wider than those given above, even as wide as nearly $11\frac{1}{2}$ octaves, or 14 to 41,000 vibrations per second (Preyer¹). The upper limit varies so much that many persons cannot hear the chirping of a cricket or the higher partial tones of sibilant sounds; and the variations in the lower limit may be compared with red blindness or Daltonism.

The term 'tone' is now restricted to those sounds, hardly ever occurring in nature, which are due to pendulum-like vibrations, and whose amplitude, therefore, is proportional to the sine of the time. Ordinary sounds consist of 'musical tones,' or those whose periodicity is well marked; and of 'noises' which are not periodic, or whose periodicity is not marked enough to constitute them musical tones.

The essence of a compound musical sound, and its analysis into simple tones, has been already discussed (p. 317). Simple tones can only be artificially produced by throwing a resonator into consonance with one of the constituent or partial tones of a compound tone, with which tone it is in tune. For such a purpose one of the resonators mentioned on p. 318, or the resonance tubes, may be employed; or a monochord, along the string of which a vibrating tuning-fork is made to slide until the string is of such length that its 'proper tone' is in unison with a constituent tone of the compound sound produced by the tuning-fork (Helmholtz).

The distinctions of quality in sensations of sound, in face of the doctrine of specific energies, can no better be explained on the assumption that one fibre is capable of stimulation in different ways, than the same distinctions in sensations of light. But since the number of distinguishable qualities is infinite, while the number of auditory fibres is limited, we must suppose, as in the analogous case of light, that a decomposition of the sound into certain simple components occurs, for each of which a simple fibre is provided. This supposition regarding the ear does not involve such important difficulties as in the eye, where all the species of fibres must further be supposed to be again collected at every colour-perceiving point of the retina; for in the ear it is only necessary that they should exist somewhere within reach of the sound-stimuli. In support of an hypothesis of a resolution of sounds in the ear and an apparatus for picking out special components, the following direct experiments may be adduced (Helmholtz):—

If two different simple tones of a given force are produced simultaneously, mutual disturbances in their wave-systems become perceptible, which give rise in sound-conducting media—e.g. the air—to new vibrations. These new vibrations are of two orders, in one of which the vibration number is equal to the *difference* between the two primary vibration numbers, and in the other to their sum. Although in this case only one resulting wave-system reaches the ear and is transmitted unchanged through the conduct-

¹ Preyer, 'Ueber die Grenzen der Tonwahrnehmung.' *Sammlung Physiologischer Abhandlungen*. Herausgegeben von W. Preyer. 1 Bd., Jena, 1877.

ing media to the nerve-endings, *four separate single tones are heard at the same time*, provided the intensity is sufficient; that is to say, two primary and two *combinational tones*. Of these last, one is the *differential tone*, the other the *summational tone*.

Whenever a compound tone is produced we recognise in it its specific composition—in other words, the *musical colour* (*Klangfarbe*), *timbre*, or ‘quality,’ which accompanies the fundamental tone. Besides this, each single constituent tone of the compound tone may, without special practice, be singled out from it by the ear, provided that immediately before the production of the compound tone the single tone has been heard.

Finally, the effect produced by the simultaneous sounding of many compound tones is not, as one might expect from the complexity of the resulting wave-systems which pass through the ear, a mere noise, for each separate tone can be clearly distinguished. Indeed, in an orchestra, one instrument can be singled out from the rest, and its sounds followed.

All these observations point to the conclusion that there is in the organ of hearing an *arrangement which resolves every wave-system, however complex, into simple pendulum vibrations*; just as every compound tone may be resolved by resonators into its constituent tones. They indicate further that every simple partial vibration excites a particular nerve fibre, and by doing so brings about the sensation of a simple tone. This supposition is raised into a certainty by the following observation (Helmholtz): If several simple tones, each beginning at a different time, in such a way that different phases of their vibrations are coincident, are combined into one compound tone, the most manifold variations of the combined wave-system result. If the auditory nerves were excited to different forms of functional activity by the wave-system as such, then the impressions of musical sounds received would vary in each experiment. But if the experiment is made with the vowel apparatus mentioned on pp. 326 and 327, it is found that in all cases the same musical sound is heard; the slightest difference would manifest itself in a corresponding difference in the vowel sound.

Every resonator answers, not only to its proper tone, but also to tones which are very near it; the further, however, the two tones are apart, the feebler is the resonance.¹ The difference, as regards pitch, at which a resonator is capable of being excited by a tone (called the range of sympathetic vibration) varies proportionately to the completeness with which the resonator is damped. The degree of damping is measured by the number of vibrations which must occur before the intensity is reduced to a definite fraction—say to one-tenth of what it was at first. On the other hand, the extent of the sympathetic vibration executed by any tone can be measured by the difference between this tone and the proper

¹ In point of fact, the strongest answering tone is somewhat different from the proper tone of the resonator; the two would only be absolutely identical if friction and resistance of the air were nil.

tone of the resonator when the former excites the resonator, as its proper tone does, but with a definite fraction, say, one-tenth of its intensity. If this difference is known, the degree of damping of the resonator can be calculated, and *vice versa*. The following Table shows the relation in which each stands to the other (Helmholtz):—

Difference of pitch (the intensity of the sympathetic vibration being reduced to one-tenth).							Number of vibrations which occur before the intensity of the tone of the resonator is reduced to one-tenth.
Eighth of a Tone	38.00
Fourth of a Tone	19.00
Semitone	9.50
Three-fourths of a Tone	6.33
Whole Tone	4.75
Five-fourths of a Tone	3.80
Tempered Minor Third ($1\frac{1}{2}$ Tone)	3.17
Seven-fourths of a Tone	2.71
Tempered Major Third (2 Tones)	2.37

The degree of damping of the resonator in the ear may be ascertained by the following experiment:—A shake, of which the beats recur ten times in a second, can be heard with perfect distinctness at all parts of the scale down to the low A (110 vibrations) without the impression of the alternation of the two tones being obliterated in the ear by the after-sounding of the vibrating parts. Below A this is the case. Assuming then that the intensity of the vibrations must sink to one-tenth in order that when the same tone recurs, that is to say, after an interval of a fifth of a second, it is no longer audible, it follows that the parts of the organ of hearing set into vibration by A after a fifth of a second, i.e. 22 vibrations, continue to vibrate with only a tenth of their original intensity. The degree of damping of the resonators in the ear must therefore correspond to about the second, or perhaps the third or fourth degree of the Table given above; and it is actually observed that below A the shake becomes rough and confused. Taking the third degree as the correct one, if the intensity of excitation of the resonator, by its proper tone, is equal to 100, its excitation by other tones approximating it in pitch will be as follows:

Difference of pitch in } fractions of a whole } Tone }	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
Intensity of sympathetic } vibrations }	100	74	41	24	15	10	7.2	5.4	4.2	3.3	2.7

The parts of the ear which are set into vibration by the note A are therefore affected with only one-tenth of the intensity by any tone which is removed half a tone from A in pitch; hence the same resonators cannot be called into action for A sharp and A flat, as for A. This is another argument in favour of the theory above quoted (Helmholtz).

The occurrence of deafness for a series of tones, *e.g.* the deepest notes (bass deafness), which is frequently observed, favours the opinion that there exist in the ear separate organs for the perception of tones of different pitch (Moos). According to this theory any simple tone would excite the particular resonator in the ear of which the proper tone is nearest to it, with the greatest intensity, those adjoining it with less.

Theoretical considerations, however, indicate that, if the membrana tympani is excited by a simple tone, it vibrates at the same time with the harmonic overtones of the exciting tone; so that the resonators answering to these overtones are excited, as well as those answering to the original tone, and therefore a simple tone is never heard (J. J. Müller).

The analysis of compound tones in the ear can only be effected by a system of resonators. It is still a matter of conjecture what part of the ear is to be regarded as constituting such a system. The cochlea claims the first consideration in this point of view. If we suppose the arches of Corti to be resonators (Helmholtz), an obvious correspondence presents itself between their gradually increasing dimensions and the graduation required in the numbers expressing their proper vibrations. Or we may take the simpler view that the rays of the membrana basilaris (Hensen), due to the greater tension of the membrane in the radial than in the longitudinal direction, correspond to a series of tense strings of gradually increasing length. According to another view, the auditory cirrhi of the labyrinth and cochlea may constitute a system of which the graduation is dependent on the varied length or stiffness of these organs (Hensen).

According to Kölliker, the cochlea contains about 3,000 arches of Corti. Deducting 200 for tones which are musically unavailable, 2,800 remain for the seven octaves that are musically audible (from C II. to H VI.) Hence there are 400 arches to each octave, and $33\frac{1}{3}$ ($=\frac{400}{12}$) to each semitone. As skilled musicians can distinguish an interval amounting to $\frac{1}{64}$ of a semitone (E. H. Weber), it may be assumed that a tone which is intermediate between the proper tones of two adjoining Corti's elements will affect both with unequal intensity, and that by this difference the pitch will be perceived (Helmholtz). Slight variations or imperfections in musical intervals are more readily detected by the ear than the mere difference of neighbouring tones; thus in a given experiment the tone 503 was distinguished from the tone 500, the interval being $\frac{1}{31}$ of a tone, while 500·4 was distinguished from 500·5 by comparison of each with the octave 1,001, although the difference was only $\frac{1}{620}$ of a tone (Preyer).

At least two vibrations following one another with rapidity are necessary to excite the sensation of a tone. A single vibration causes only the impression of a tap. If, for example, a card is held against the teeth of a revolving Savart's toothed wheel, so as to produce sound, the tone is unaltered so long as the rate of revolution remains the same. If, now, all the teeth excepting the last two are gradually removed, the same tone continues to be heard, although it becomes duller, just as a colour becomes duller when mixed with a good deal of 'black.' If the last tooth but one is removed, the tone vanishes and only the sensation of a tap remains, which is to be regarded as a rapidly vanishing wave-system.

If many different simple tones are so combined that the organ of hearing cannot analyse them, or if they follow each other so rapidly that the after-tones of each preceding tone are mingled with those of its successor, so that a confusion arises which cannot be analysed by the ear, and in which no periodicity can be perceived, the resulting sensation is commonly called a noise. Many noises, therefore, are only very complicated musical sounds, in which a fundamental or prime tone, having often the timbre of a vowel, can be recognised. According to the vowel sound heard,

these noises receive names by onomatopoeisis, such as clicking, thundering, clattering, crackling, &c. Besides these apparently unperiodical sound vibrations (which, however, must needs be possessed of periodicity, seeing that they are composed of tones), there are others which are really unperiodical, and to the impression on the ear of these the term noise should be exclusively applied (Helmholtz). In what parts of the organ of hearing the perception of taps and noises takes place is at present matter only of conjecture without proof.

The mingling of successive tones would be much more constant, and music would be therefore impossible, if the damping of the vibrating parts of the ear were not very complete. The damping apparatus has not yet been thoroughly investigated. It has been supposed by some that the otoliths and the *membrana tectoria* of the cochlea, which lies upon the organ of Corti, constitute damping apparatus (Waldeyer).

Harmony of Musical Sounds.

If several musical sounds reach the ear at the same time, an agreeable or disagreeable impression is received, the nature of which is ultimately connected with the relations of the vibrational numbers of their prime tones. According to these relations we distinguish consonant (agreeable) and dissonant (disagreeable) combinations of sounds. The octave ($1 : 2$) and the twelfth ($1 : 3$) are the most perfectly consonant sounds; then follow in order in the direction of dissonance, the fifth ($2 : 3$), fourth ($3 : 4$), major sixth ($3 : 5$), major third ($4 : 5$), minor sixth ($5 : 8$), minor third ($5 : 6$), &c. The explanation of this phenomenon is that the disagreeable impression of a dissonance consists in the beats caused by it, i.e. in the variations of intensity produced by the interference of two wave-systems which differ somewhat in their wavelengths. Two simultaneous tones of different pitch strengthen each other whenever the wave crests or the wave troughs between them coincide, and they weaken or annul each other when crests coincide with troughs. The periods of recurrence of beats must obviously be equal to the difference between the vibration numbers of the two tones; the smaller the interval between the two tones and the lower the pitch, the less frequently do the beats occur. If they are so frequent that they cannot be recognised separately as beats, they give the impression of a painful discontinuity (comparable to the flickering of a light). The maximum of confusion and roughness is experienced when the beats recur thirty-three times in a second. The more nearly the constituent tones of two simultaneous compound tones coincide with each other or with combinational tones so as to give rise to beats of moderate frequency, the greater will be the discord.

For further explanation attention is directed to the Table, which, starting from the prime tone C (256 vibrations), sets forth

Compound Tones	Vibration Numbers of Partial Tones and Beat-Numbers										Smallest Beat-Numbers	Degree of Consonance	
	256	512	768	1024	1280	1536	1792	2048	2304	2560			
Prime tone c^I 256													
Octave c^{II} 512		512		1024		1536		2048		2560	No beats	Absolute	
Twelfth g^{II} 768			768			1536			2304				
Fifth g^I 384	384 128 128		768	1152 128 128		1536	1920 128 128		2304		$128 \dots = \frac{256}{2}$	Perfect	
Fourth f^I 341	341 85 171 171 85	1024			1365 85 171 171 85	1707	2048		2389 85 171		$85 \dots = \frac{256}{5}$	Medial	
Major sixth a^I 427	427 171 85		853 85 171	1280		1707 171 85	2133 85 171		2560				
Major third e^I 320	320 64 192 128 128 192 64	640	960	1280		1600 64 192 128 128 192 64	1920 128 128 128 192 64		2240	2560	$64 \dots = \frac{256}{4}$	Imperfect	
Minor sixth g^I 410	410 154 102	819	1229 51 205 205 51			1638 102 154	2048		2458 154 102		$51 \dots = \frac{256}{5}$		
Minor third d^I 307	307 51 205 102 154 154 102 205 51	614	922	1299 51 205 102 154 154 102 205 51		1536	1843 51 205 102 154 154 102	2150	2458				
Major seventh h^I 480	480 224 32	960	192 32		1440 160 96		1920 128 128		2400 96 160		$32 \dots = \frac{256}{8}$	Dissonance	

the vibration numbers of its constituent tones, as well as those of some of the tones derived from it. If all the conditions of dissonance were given, the Table would also exhibit the combinational tones, which, are, however, not here taken into consideration. The small figures denote the number of beats which a constituent tone makes with the two constituent tones of the fundamental compound tone (*Grundklang*) which are nearest to it.

It is seen from the Table that in the sounds of the octave and twelfth there are no constituent tones, except those which are also in the fundamental sound: here therefore no beats are possible—the octave and twelfth are in ‘absolute’ consonance. In the sound of the fifth, constituent tones exist which are not in the fundamental tone, but these are not brought into such collision with those of the fundamental tone nearest to them as to cause beats; the fifth therefore is a ‘perfect’ consonant. The conditions, however, for beats exist in the constituent tones of the fourth, major sixth and major third (‘medial’ consonances), and in an even greater degree in those of the minor sixth and minor third (‘imperfect’ concords), and still more in those of the seventh, second, &c. (dissonances). It is also seen that the number of beats gradually approaches 33. Dissonance is occasioned by any interval, the more readily the lower the pitch. (Compare the statement above.) On these principles rest the sciences of harmony and temperament, which cannot, however, be entered upon here. The relation of constituent tones (their ‘melodic relationship’) is also important with regard to the succession of sounds which constitutes melody. If a sound is followed by its octave, no new tone is heard, the attention is not attracted by any new impression. The contrary is the case when a note is followed by its fifth or fourth, &c.

If a compound tone, of which the prime tone makes n vibrations in a second, is heard along with others, the smallest number of beats per second depends on the relation between the two tones, as follows:—The fundamental tone in simultaneous vibration with the fifth gives $\frac{n}{2}$ beats, with the fourth and major sixth $\frac{n}{3}$, with the major third $\frac{n}{4}$, with the minor sixth and minor third $\frac{n}{5}$, with the major seventh and major second (a whole tone) $\frac{n}{8}$, with the minor second, (semitone) $\frac{1}{16}n$, &c. This may be more generally expressed as follows:—If n represents the vibrational number of the deeper fundamental tone, and m that of the higher, and the fraction $\frac{m}{n}$ is reduced to the smallest whole numbers ($\frac{m'}{n'}$), then the minimum number of beats is $= \frac{n'}{2}$. In other words, the smaller n is (that is, the lower pitch) and the greater n' is (that is, the more incommensurable the fraction which expresses the interval), the smaller is the minimum number of beats per second.

The fraction $\frac{m'}{n'}$ is clearly $\frac{2}{3}$ for the fifth, $\frac{3}{4}$ for the fourth, $\frac{5}{3}$ for the major sixth, $\frac{5}{4}$ for the major third, $\frac{6}{5}$ for the minor sixth, $\frac{6}{4}$ for the minor third, $\frac{7}{3}$ for the major seventh, $\frac{9}{8}$ for the major second, $\frac{16}{15}$ for the minor second.

A simple experiment shows convincingly that the essence of dissonance really lies in the beats. If one of two perfectly similar tuning-forks, standing on resonance cases, is put more and more out of tune by means of wax, beats of increasing frequency are heard on sounding them; when those beats reach a certain rate of frequency the characteristic sensation of discord is perceived.

Reference of Auditory Impressions to the Exterior.

The cause of every sensation of sound which is transmitted by the membrana tympani appears to the mind to come from outside, whereas that which is conducted through bone appears to arise in the head itself. If, *e.g.*, the head is held under water the impressions of hearing will only seem to come from outside when the external ear is filled with air (Weber). As, however, even in this case the principal conduction is by means of the bones in the head, the impression of extrinsic origin is occasioned by the sensibility of the membrana tympani, and is not due to any peculiarity imparted to the labyrinth waves emanating from the stapes. If this be so, one may suppose that the sensibility of the membrana tympani gives information as to the direction of the sound-waves which reach it, and perhaps this is also the case as regards the pinna, which from its numerous projections is peculiarly adapted to judge of the angle at which the sound rays fall (Weber), especially when it is aided by its movements. (Compare what follows.)

Subjective Sensations of Hearing.

In the organ of hearing, as in that of sight, there are certain 'subjective sensations,' which depend either upon peculiarities in the excitation of the nerve, or upon abnormal conditions of the nerve itself. These impressions, however, appear to be of very limited occurrence, and have been as yet but little investigated. With reference to after-tones, it may with probability be concluded that when a series of tones succeed each other with rapidity (as, for example, when the teeth of a Savart's wheel are so set that, instead of being equidistant throughout, they are at different distances from each other in successive segments of the circumference), a noise is produced by the mixture of tones which is analogous to the mixture of colours in the colour top; nevertheless, it should be kept in mind that the after-tones may in part be due to the continued resonance of the special resonating structures of the ear. 'After-sounds' are to be regarded as physical phenomena, as for example when a tone or a piece of music rings in the ear long after the sound has ceased to be actually heard. This is also true of other hallucinations of hearing.

Amongst subjective impressions may be mentioned ringing and humming in the ears. These tones or noises are dependent upon the excitation of the auditory nerves by unknown causes, and are particularly apt to occur when their excitability is morbidly increased. The subjective musical tones which are occasionally observed may probably be explained as arising from abnormal excitation of the nerve fibre corresponding to a single element of the organ of Corti; for in these cases there is at the same time excessive sensibility to the objective sounds which correspond to those heard subjectively (Moos, Czerny, Samelson).

Entotic Impressions.

From subjective sensations may be distinguished those impressions which have their source in the organ of hearing, and are therefore called *entotic*. To these belong, 1, rushing sounds caused by vibrations of the air in the external ear, or in the cavity of the tympanum, when their communication with the atmosphere is interrupted—in the case of the former by substances covering it, or inserted into it, or by cerumen; in that of the latter, by occlusion of the

Eustachian tube. These sounds in the external ear are particularly loud when a hollow body, such as a tube, in which the air vibrates, is applied to the auditory passage, so as to lengthen it; and they are undoubtedly due to the fact that, under these circumstances, conduction through bone is more perfect, and hence the muscular sounds generated in the muscles of the head, and the frictional sounds arising in the blood-vessels, &c., are more readily perceived. 2. The crackling sound caused by contraction of the tensor tympani, as to the significance of which see p. 440. 3. Hammering sounds, caused by the pulsation of the arteries either in the organ of hearing, or at a distance from it. These become more audible when the head rests upon a hard body. 4. Friction sounds, caused by the circulating blood. 5. Muscular sounds, &c.

Binaural Audition.

By hearing with both ears, as by seeing with both eyes, the two organs are enabled to assist each other mutually and to correct each other's errors. We are also thereby aided in determining the locality of sound-producing bodies. Whether the terminations of the organ of hearing possess anything corresponding to the 'identity' which exists in the eyes, whether for example, the excitation of two corresponding fibres of both cochleæ is perceived as a single sensation, cannot at present be decided. A single tone, although it is heard by both ears is heard only as one, in which case we may assume that the elements in the two cochleæ which are affected by it correspond with each other. On the other hand, we can distinguish two tones even when both ears are excited simultaneously by tones of the same pitch, provided that either their intensities are different or that the excitability of the two corresponding elements is unequal. This last statement is proved by the following experiment. If two similarly sounding tuning-forks are held one before each ear, and one of them is made to revolve round its axis in such a way that the tone shall alternately vanish and reappear (four times in one revolution), neither fork is heard continuously, but both sound alternately, the fixed one being only audible when the revolving one is not heard (Dove). The excitability naturally diminishes during the continuance of the sound, but less on the side of the revolving tuning-fork than on the other side. If the excitation is of equal intensity, the impression of a tone will be perceived only on the side on which the excitability is greater. (This result is of course not obtained when the two tones are different.) From this experiment it may be concluded either that the excitations of two corresponding elements of both ears can be distinguished from each other, or that the excitation is perceived as a single one, but is referred to the side on which the excitation is strongest. Both conclusions are opposed to the admission of an analogy with the organ of sight. The value of the experiment is, however, diminished by the circumstance that in all probability the sounds of the two forks are not absolutely identical. Another fact which appears to militate

against the notion that we perceive excitations of both ears in common, is that in most persons (Fessel, Fechner), and especially in pathological conditions (v. Wittich) one ear perceives the same tone at a higher pitch than the other.

Appreciation of Direction.

Two opposite membranæ tympani and pinnæ must naturally afford a more accurate indication of the direction of a sound than one alone, considering that by turning the head we can alter the relation of the ears to the sounding body. It is even conceivable that the different local relation of the two ears to objects might enable us to judge of distance. The position of the ears is best adapted for the discrimination of sounds coming from the sides. Those from before or behind can only be distinguished by turning the head or by the position of the pinnæ, the situation of which is best adapted for the reception of waves coming from the front. These are therefore heard more loudly than those from behind. If the pinnæ are pressed against the head and the hands placed before the external meatus, so as to form a kind of ear, sounds coming from behind are heard more loudly than they would be otherwise.

It is conceivable that in the conduction of sound through the bones the differently directed systems of waves would stimulate unequally different parts of the ear. The semicircular canals, which are arranged in three co-ordinate planes at right angles to one another, probably are concerned in the appreciation of the direction of sounds; as is rendered specially probable from the occurrence of certain peculiar movements after injuries inflicted upon individual canals (Flourens¹). Further information upon these phenomena and upon their significance will be furnished at the end of this chapter.

Protective Organs of the Ear.

In a certain sense the pinnæ, especially in animals where they are mobile, may be regarded as protective organs for the ears, inasmuch as the existence of projections (*e.g.* the tragus in man) tends to hinder the penetration of dust or cold air into the ear. Other protective organs are the stiff bristly hairs (*vibrissæ*) of the external meatus, and the ceruminous glands, the secretion from which lubricates the wall of the meatus. The purpose of the cerumen is uncertain. Its absence determines difficulty of hearing and buzzing in the ear, the cause of which is unknown. The internal ear, from its position inside the petrous bone, is completely protected.

¹ Flourens, *Recherches expérimentales sur les propriétés du système nerveux*. 1842.

III. THE OLFACTORY ORGAN.

The peripheral terminal organs of the olfactory nerves pass as numerous branches through the foramina of the cribriform plate of the ethmoid into the cavity of the nose, and are expanded on a membrane, which, as a mucous membrane, lines the upper part of the nasal cavity, and is distinguished from the mucous membrane proper of the nose (Schneiderian membrane) by its lighter colour and the absence of the ciliary epithelium. These terminal organs are excited by certain gaseous bodies in a manner at present totally unknown, nor do we know the properties to which they owe their excitability. The odorous particles are conducted to the olfactory membrane by inspiration through the nose. The inspired current is split up at the anterior prominent ridge of the inferior turbinated bone, and a part of it, instead of passing directly along the inferior meatus to the posterior nares, takes a circuitous course along the upper parts of the nasal cavity (Bidder). The excitation, it appears, takes place only at the first moment of contact, for to ensure a more permanent sensation it is necessary that fresh particles of the exciting body should be brought continually in contact with the terminal organs, or, in other words, that the particles should pass in a current through the olfactory organ, and the effect is greater the quicker the renewal of the particles takes place, *i.e.* the more rapid the current.

The olfactory bulbs, which were formerly considered as a part of the olfactory nerves, are now more properly considered to be parts of the brain. The olfactory nerves proper are distinguished from other nerves by consisting of a number of small bundles, each of which again is composed of numerous, extremely fine primitive nerve-fibres, surrounded by a common areolar membrane. The olfactory membrane which lines the two upper turbinated bones and the upper part of the septum ('*regio olfactoria*') has the following construction (M. Schultze): Between the cylindrical epithelial cells, pointed at their basal end, there are found bipolar spindle-cells, which send one process to the surface and another into the interior; the latter is said to be identical with the delicate primitive nerve-fibres of the olfactory nerve, the other process is provided with a bundle of very long tender hairlets, which project beyond the surface; the spindle-cells are thus considered to be nerve-cells. According to recent researches (Exner), the cells found in the frog, and formerly described as simple epithelial cells, are likewise nerve-cells and are provided with hairs.

That gaseous bodies only possess the power of exciting the olfactory organs is evident from the fact that the filling up of the nose with an odoriferous (volatile) fluid, such as eau-de-Cologne, produces no sensation of smell (Weber). It is well known, also, that the body to be smelled must pass through the olfactory region in a current, for every sensation of smell can be at once stopped by holding the breath or by inspiring exclusively through the mouth, even if the atmosphere, and therefore also the air in the nasal cavity, be filled with the odorous substance. On the other hand, rapid and repeated respirations ('sniffing') increase the impression of smell.

The necessity of the conveyance of the current to the olfactory region by the anterior promontory of the inferior turbinated bone is seen from the fact

that the odorous body is not smelled when first passed into the mouth and thence *through the* posterior nares into the nose (Bidder). Most of the odorous substances act even when diluted to an extraordinary extent, so that an exceedingly small quantity mixed with the atmosphere of the room can readily be perceived. Recently it has been shown that most of the odorous vapours possess a large capacity for absorbing heat (Tyndall).

The Sensations of Smell.

Excitation of the terminal olfactory organs, possibly also an excitation of any kind of the nerve-trunks themselves, gives rise to certain sensations, which we call odours. They are distinguished both as regards their intensity and character. The intensity seems to depend—1. On the quantity of odorous body in the gaseous mixture. 2. On the velocity of the ~~current~~ passing through the olfactory region. 3. On the number of excited olfactory elements. It appears at least that those animals possess the most delicate perception of smell whose olfactory organs cover a large surface. The cause of the special character of an odour is totally unknown, and we possess no division nor scale, nor even a name for the different odours, but call them only after the body to which they belong, and of which the same or similar character of the smell reminds us.

It is scarcely doubtful, after the analogy of all the other sense-organs, that mechanical, electrical, &c., irritation of the olfactory nerve produces the sensation of smell; experimentally this has, however, as yet not been proved. The only sure way to direct electric currents to the olfactory nerves would consist in filling the nasal cavity with water, into which one of the two electrodes is inserted; but here the simultaneous irritation of the sensible fibres of the trigeminus produces such violent pain, that we cannot decide as to the sensations of smell produced at the same time (Rosenthal). In the excitation of the terminal organs of the olfactory nerve by odorous substances, the hairs on the cells above described seem to take an important part; this seems probable from the fact that by filling the nasal cavity with water¹ the sense of smell disappears for a short time (E. H. Weber). Some have also observed that by the contact of these hairs with water they swell up, and are invisible for some time (Schultze).

The principle of specific energies (p. 351) would justify us in assuming here also the same as has been shown for the organs of sight and hearing (pp. 404 and 446), the existence of different olfactory fibres, each of which would be excited by a particular kind of olfactory stimulus and give rise to a particular sensation; we possess at present no clue whatever as to how many such fibres are likely to exist.

From the olfactory sensations proper we have to distinguish those impressions which depend on the irritation of the sensory fibres of the fifth nerve present in the nasal mucous membrane; thus ammoniacal vapour acts on the latter chiefly, and is therefore still perceived as a sensation after the olfactory terminations have been destroyed, or it may cause reflex actions (sneezing).

We know very little about subjective sensations of smell; in certain patho-

¹ In filling the nasal cavity with fluids these are poured in through the nares, the body taking up the recumbent posture, resting on the back. The fluid is prevented from running out through the posterior nares by the velum palati, which adapts itself to the wall of the pharynx (E. H. Weber).

logical conditions of the nose (catarrh, &c.), the sense of smell is for a time quite suspended, or even replaced by abnormal sensations of smell.

About '*after-smells*' we know next to nothing. The author observes that for several hours after experiencing certain strong odours, such as cadaverous odours, every unpleasant smell has, with him, most distinctly the character of the first.

As regards the relations of the two nasal cavities to each other, we only know that the simultaneous irritation of the two by different odours does not give rise to one impression, but causes a sort of race between the two (Valentin).

The nasal mucous membrane may be considered to act as a protecting organ to the olfactory region, by liberating the traversing air from its coarser noxious admixtures. On the other hand, the olfactory organ may be considered as keeping guard for the respiration, inasmuch as many of the noxious impurities of the atmosphere affect the sense of smell.

IV. THE ORGAN OF TASTE.

Our knowledge of the sense of taste is more fragmentary than that of any other sense organ. The seat of this sense has not even been accurately fixed, and for the following reasons:—1. Because it is difficult to separate this sensation from other sensations which are evoked at the same time on the application of the substance to be tasted, namely odorous and tactile sensations. 2. Because fluids which possess a taste pass so easily from any one spot of the mouth, and therefore possibly from a spot not endowed with taste to the proper taste organs. The special seat of the gustatory sensibility has therefore been very differently stated. Undoubtedly the root of the tongue plays an important part, but it is doubtful whether it alone (Bidder, Wagner), or also the tip and the borders of the tongue (Schirmer, Klaatsch and Stich, Camerer), the soft palate (J. Müller, Drielsma), or at least a part of it (Schirmer, Klaatsch and Stich), or even the hard palate (Drielsma), are seats of gustatory sensation. Researches with limited electric irritation (Neumann) show the tip of the tongue and its borders over an area of several lines to be capable of appreciating taste, though not all qualities of taste (Lussana); the anterior part of the upper surface, the whole of the lower surface, and the frænum are devoid of gustatory sensitiveness.

The *nerves* presiding over taste seem to belong to several cranial nerves. Besides the glosso-pharyngeal nerve, about whose function there can be no doubt, the lingual branch of the fifth is considered by many to be a nerve of taste, though some observers believe that it derives its gustatory fibres from the chorda tympani branch of the facial nerve; the rami palatini of the fifth are likewise considered to be gustatory.

In facial palsy disturbances of taste are very common. Against the participation of the facial nerve it is asserted that, after section of the chorda tympani,

no degenerated nerve-fibres are to be found in the lingual nerve beyond the point of departure of the salivary nerves (Vulpian); others, however, have found such degenerated nerve-fibres (Prevost) (in the dog even, Vulpian). Since a case was recorded in which the intra-cranial portion of the facial nerve was found totally degenerated without there having been any disturbance of taste (Wachsmuth), it has been assumed that the gustatory fibres [from the glossopharyngeal nerve] join the facial nerve by the N. petrosus superficialis major and enter the course of the fifth partly by the N. petrosus superficialis minor

FIG. 67.

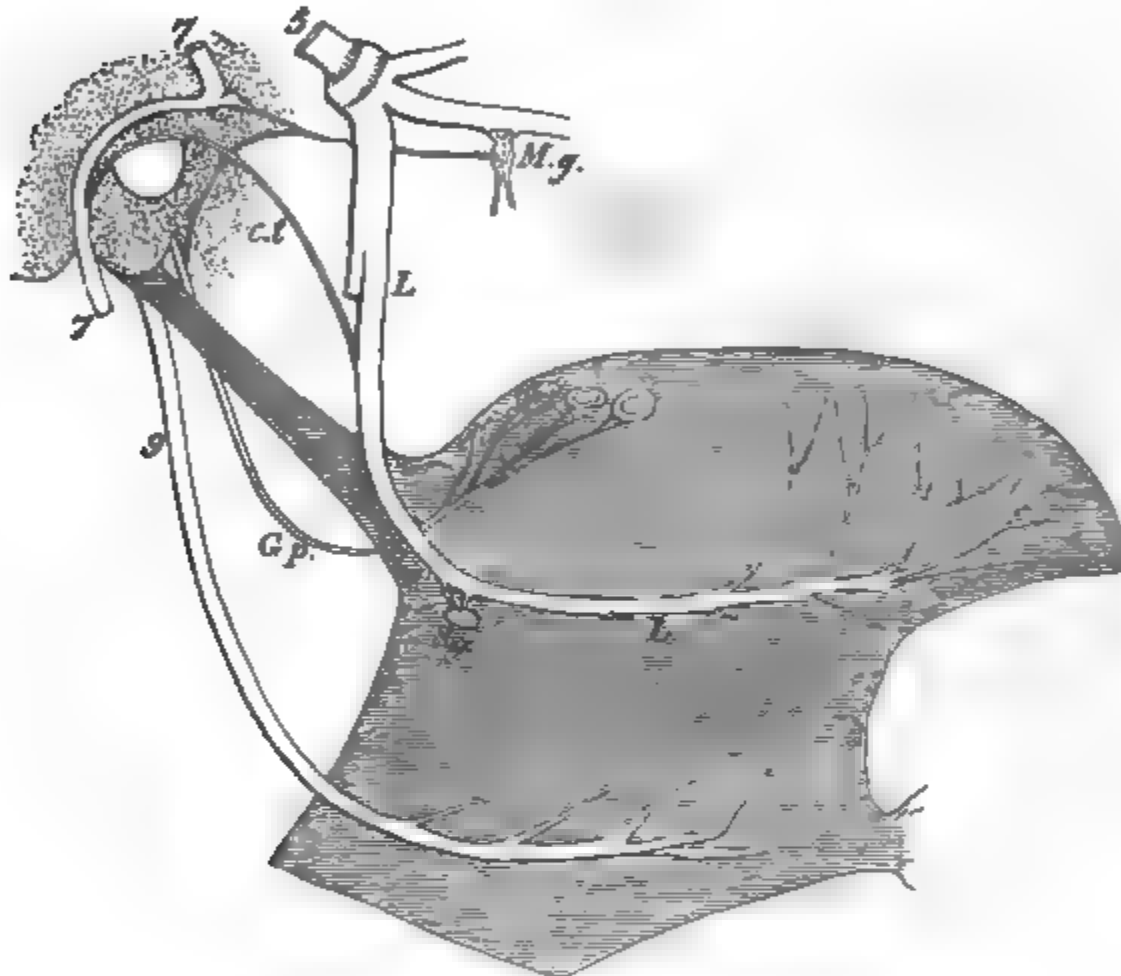


DIAGRAM OF THE NERVOUS SUPPLY OF THE TONGUE.

5. The fifth nerve. *L.* Its lingual or gustatory branch, supplying the anterior part of the tongue with sensibility.

7. The facial nerve, or portio dura of the seventh, giving off at its bend the great superficial petrosal nerve to Meckel's ganglion, *M. g.* *c. t.* The chorda tympani nerve, passing from the facial to the lingual branch of the fifth. *S. g.* The submaxillary ganglion. *G. p.* The glossopharyngeal nerve going to the back of the tongue and the circumvallate papillae; a small twig passes from it to the great superficial petrosal nerve.

9. The hypoglossal nerve; the motor nerve of the tongue.

and the otic ganglion, and partly by the chorda tympani (Schiff). Since also we may have paralysis of the fifth without disturbances of taste, it is the more probable that fibres of the glossopharyngeal nerve pass by means of Jacobson's anastomosis (N. petrosus superficialis minor and the otic ganglion) into the fifth. It is worthy of notice that both the nerves of taste contain also vaso-dilator fibres for the mucous membrane of the tongue, the *chorda* for the anterior, and the glossopharyngeal for the posterior region.

The terminal organs of the nerves of taste are found in the papillae of the tongue. The furrow surrounding the circumvallate papillae at the root of the tongue dips down, and forms a capillary

space, the inner side of which is provided with the terminal organs of the gustatory nerves, while the free surface of the papillæ shows the ordinary structure of the mucous membrane of the tongue; these terminal organs are the *gustatory bulbs*, or 'gustatory goblets,' and consist of goblet-like organs, open externally, and filled with cells; of the cells themselves those more centrally situated, 'the gustatory cells proper,' terminate peripherically in a short rod, while their central ends pass into fine nerve-fibres, which, in the interior of the papillæ, are connected with medullary nerve-fibres (Lovén, Schwalbe). The fluid to be tasted must therefore first enter the capillary spaces mentioned. These spaces containing the gustatory bodies are found also in the form of plane surfaces in the *papillæ foliatæ* of man, and most animals (generally there is one at each border of the posterior part of the tongue, while in man it consists again of five parallel longitudinal rows; C. Mayer, Krause, and v. Wyss). The fungiform papillæ possess gustatory bodies on their upper surface (Lovén, and, according to some, the free surface of the papillæ circumvallatæ is also provided with them (Schwalbe, Hönigschmied).

In the vicinity of the *papillæ vallatæ* and *foliatæ* there occur peculiar acinous glands of small size which furnish a secretion containing no mucus; these so-called 'serous glands' occur besides in the nose (Heidenhain), and possibly possess some function in relation to the excitation of gustatory impressions (v. Ebnér).

The gustatory nerves are excited by certain substances which are fluid, or at least soluble in the fluids secreted in the oral cavity; probably also most (Stich) gases which possess any taste belong to this class. The process of excitation is totally unknown. 'Gustatory sensations' are the results of the excitation of the terminal organs as well as of the trunks of the gustatory nerves themselves, and these are distinguished both as to their intensity and character. The intensity of the sensation depends on the force and duration of the excitation, and the number of excited nerve fibres. If the excitation be, therefore, caused by a sapid substance, then the taste will be the more intense—1, the more sapid the substance is; 2, the more concentrated it is; 3, the longer it acts; 4, the larger the surface of the taste organ it is in contact with; 5, the more easily excited the nerve fibre. The properties ~~are~~ not known by means of which the tasting substance produces the different empirical and undefinable characters of taste which are known, such as sweet, bitter, acid, alkaline, salty, putrid; the different sweet-tasting bodies (*e.g.* the different kinds of sugar, glycerin, glycine, salts of lead, beryll-salts, &c.) belong to the most varied groups, and show no relations in their other properties.

As regards the taste of substances of the different chemical groups, the following facts may be noticed: the sour taste of the soluble acids; the sweet taste of all polyatomic alcohols, which contain as many OH- groups as they

contain C atoms (to this group belong $C_2H_4(OH)_2$, Glycol.; $C_3H_5(OH)_3$, Glycerin; $C_4H_6(OH)_4$, Lichen-sugar; $C_6H_8(OH)_6$, Mannite [less 2H Grape sugar]); the bitter taste of many compound sugars (glucosides), many alkaloids, &c.

In man the excitation of the trunks of the gustatory nerves can only be effected by electricity. If an ascending current be passed through the gustatory nerves (as by putting the positive electrode to the tip of the tongue, the negative electrode being in contact with any other part of the body, say the hand), a distinctly acid taste is perceived; if the current is a descending one, the taste becomes burning and 'alkaline.' If now, in this case, we had a direct excitation of the nerves by the current, the production of different tastes, according to the direction of the current, would speak against the principle of specific energies (p. 351). It has, therefore, been attempted to explain the results as due to the tasting of the electrolytic products separated out on the tongue. The observation that the results remain the same when the current is passed to the tongue, not by immediate metallic contact but by the interposition of moist conductors, does not disprove this explanation, because at the boundary of two moist conductors, and especially between nerve contents and membrane, electrolytic products are deposited.

Besides gustatory sensations, the excitation of the nerves of taste causes, in a reflex manner, secretions of the salivary glands.

We know nothing definite about subjective gustatory sensations, though their existence is demonstrated ('after-taste,' &c.) Here, too, we have to distinguish between the subjective gustatory sensations and those sensations which depend on certain conditions of the buccal mucous membrane ('perverted' tastes in catarrh, &c.)

V. THE REMAINING SENSE-ORGANS.

The perceptions produced by the other centripetal nerves (excepting the optic, auditory, olfactory, and gustatory nerves) are known as 'common sensations.' Sensory nerves are found in almost every part of the body, but not to the same extent; the intestines seem to contain the least, and the muscles, bones, fasciæ, &c. are but sparingly provided with them; most numerous, however, they are distributed over the skin and the adjoining mucous membranes (the mucous membrane of the oral and nasal cavities, the conjunctiva, &c.)

The terminations of the sensory nerves are only known for a few localities, and their minute structure is, as yet, the subject of much contention. The following forms have hitherto been described:—1. Pacini (Vater's) corpuscles; they are relatively large ($0.5-4^{mm}$), and are situated on the subcutaneous cellular tissue, especially of the hollow of the hand and foot; they are also found in the genital organs, many muscles and joints, and in the sympathetic plexus of the abdomen (for instance, in the mesentery of the cat). They are egg-shaped, and consist of many concentric lamellæ of areolar tissue, enclosing a cylindrical body, consisting of protoplasm (inner bulb); into this the nerve-fibre enters, runs along its interior as a simple axis-cylinder, and terminates, often after splitting up into several branches, in a button-like swelling extremity. The nerve-fibre, before it enters the corpuscle, is surrounded by a *lamellated* neurilemma. 2. Terminal nerve bodies (Krause's corpuscles) are oval or more or less rounded vesicles of $0.03-0.06^{mm}$, consisting of an areolar sheath, with nuclei and soft homogeneous contents, in which the nerve-fibre runs, terminating in a point; they are found in many organs, especially in the

mucous membranes, where they occupy the areolar mucosa. Possibly the organs mentioned under 1 and 2 are mere modifications of the same form of which the last-mentioned most likely presents the primary type. 3. '*Tactile corpuscles*' (Wagner and Meissner). They are found in some of the papillæ of the cutis (the rest of the papillæ contain capillary hoops), more particularly in the hollow of the hand and sole of the foot; they form elongated, oval clubs, coarsely and irregularly striated, 0·05–0·1^{mm} long, which take up nearly the whole papilla, and into which one or two nerve-fibres or parts of a nerve-fibre enter: the mode of termination of the entering nerve is, as yet, doubtful; some believe that they split up into branches and that each branch is again broken up into small transverse branchlets, which are the cause of the transverse striation; a more recent view, however, is that the tactile corpuscle consists only of a nerve-tube assuming the form of a skein; such '*terminal nerve bundles*' are seen distinctly and well developed in the glans penis (Tomsa). In the interior of the corpuscle, the branches of the nerve-fibres are said to terminate in a manner similar to that observed in the Pacinian body (Grandry). 4. '*Terminal nerve-buds*.' The terminations of the sensory nerves of the cornea. Here the nerves break up into fine branches, which form a network in the subepithelial layer, and thence send filaments, sometimes branched again, into the epithelium, and which terminate on the free surface, floating in the lacrymal fluid (Cohnheim); according to others, these filaments terminate when yet within the epithelium in a small knob (Hoyer). A similar mode of termination seems to hold good for the sensory cutaneous nerves (Langerhans, Podcopaew, Eberth). The mode of termination of the sensory (and reflex) nerves, in many places, is as yet unknown. Ganglionic bodies are observed in the skin which may possibly be terminal organs of sensory nerves (Tomsa). There are, also, special terminal organs, some of which are connected with tactile hairs, as, for instance, in the web of the bat, ear of the mouse, snout of mole, &c.

Qualities of the Sensations under consideration.

Any intense excitations of the nerves under consideration, which are distinguished as the '*sensory nerves*' in the limited sense of the word, from the preceding nerves of special sensibility, is felt as an unpleasant sensation, as *pain*, whether the terminal organs or the trunks of the nerves be excited. A large proportion of these nerves—namely, those supplying the intestines, the bones, the vessels, &c.—seem excitable only by '*pathological*' agencies, and then always to cause pain, if their function be not to call forth reflex actions. The rest, however, give rise, when their end organs are normally and not so strongly excited, to various sensations. The excitation of the end-organs may be brought about by very different processes, by chemical, mechanical, and thermal agents, and not by the vibrations of light and sound. This harmony of the specific excitants with the general nerve irritants, favours the idea that the end-organs of the sensory nerves are of simple construction, and not very different from the nerve trunks, and perhaps only made more accessible to the exciting processes of the external world by their position. The sensations which are produced by mechanical irritation of the end-organs are called *Tactile sensations*; those which follow thermic irritation, *Sensations of temperature*.

Recent observations have made it very doubtful, whether painful irritations of the skin are merely due to a stronger irritation of the ordinary nerve terminations, or whether rather to an irritation of special end-organs. For there seem, according to some observers, to be different roads of conduction in the brain, both for tactile sensations and painful sensations, such, for instance, as are caused by chemical irritation of the skin (*tactile* and *pathic* channels, see Uhap. XI.); it is possible, therefore, that in these two cases, different peripheral apparatus may be concerned, and it has, moreover, already been stated that the modes of termination of the nerves in the skin are various.

The following experiment (E. H. Weber) proves that sensations of temperature can only be caused by the thermic irritation of the *end-organs*. If the elbow is dipped into a very cold fluid, the cold is only felt at the immersed part of the body (where the fibres terminate); pain, however, is felt in the terminal organs of the ulnar nerve, namely, in the finger points; this pain, at the same time, deafens the local sensation of cold. This experiment serves, likewise, to prove that the cause of excitation is referred to the end-organ.

Tactile Sensations.

Tactile sensations are produced by mechanical irritation of different degrees, by contact and by pressure.

The limit at which the intensity of the irritation becomes painful is different for different parts of the body. By help of the tactile sensation we are able to come to the following conclusions:—1. We conclude as to the existence of a foreign body touching our body. 2. From the intensity of the sensation we estimate the intensity of the pressure exerted, and from this we estimate, under given circumstances, the weight, tension, &c. of the touching body. The muscular sensation is an important aid in these estimations (*i.e.* the sensation of the degree of exertion in the muscles concerned in carrying, lifting, drawing, pressing; see below). 3. We have always an idea of the state of irritation of all our sensory fibres, and feel therefore our whole body surface as a ‘tactile field,’ similar to the field of vision (compare p. 408). We are thus enabled to determine immediately the locality of each part touched, and thus also the position of the touching body. 4. When a body touches a cutaneous surface, or several cutaneous points simultaneously, we are enabled from the position of the different points of contact, from the different pressure, and from the spaces not touched, to draw conclusion as to the configuration of the touching body. This conclusion becomes still more positive when we pass the skin over the touching body, and thus create for ourselves a number of tactile pictures. For this purpose those cutaneous surfaces are best fitted which possess great mobility, and contain numerous sensory end-organs, *i.e.* the finger-tips, the point of tongue (see below). If different parts of the cutaneous surface touch the same body, a knowledge of the relative position of the different cutaneous surfaces is necessary in order to determine the configuration of the

touching body. This knowledge we obtain through the muscular sensation (see below), because muscular movements are necessary for nearly every change of the relative position. If this knowledge is wanting, as, for instance, in abnormally distorted displacements of position, false conceptions arise about the configuration of the body. The 'experiment of Aristotle' belongs to this class: By placing the middle finger so over the index finger that a small round body (pea, penholder) can be brought or rolled about between the radial side of the index finger and the ulnar side of the middle finger, the sensation of *two* round bodies is produced, because one body cannot be brought in contact with these two surfaces without producing distortion. By its very uniform touch we conclude the presence of a fluid, and by the more or less increasing pressure, when the tactile surface moves about, we estimate the more or less soft or hard consistency of a body, &c. These different conclusions are often enumerated as specific 'senses' (*Sense of pressure, sense of locality, &c.*)

The sensitiveness of each part of the body depends: 1. On the larger or smaller number of the end-organs connected with the sensory nerves of the part. 2. On the absolute sensitiveness of these nerves.

The *number* of end-organs in the different cutaneous surfaces can only be determined anatomically; experimentally, however, we can get relative data as to their distribution; the method is the following (E. H. Weber, Czermak): 1. Find the smallest distance which can intervene between two bodies touching the skin, either simultaneously or shortly after one another, in order to produce two separate sensations: the instrument used consists of a pair of compasses with blunt points, which can be placed on the skin at different, easily read off, distances (the eyes being shut). The distance is found to be smallest on the tip of the tongue (1.1^{mm}), on the palmar side of the third phalanx (2.2^{mm}), and the red surface of the lips (4.4^{mm}); largest on back, chest, neck, and extremities ($35\text{--}66^{\text{mm}}$).

The smallest required distance is in some places, for instance on the extremities, less in the transverse than in the longitudinal direction; it is less also when the points are placed on the skin one *after* the other; it is less when beginning with larger distances and gradually finding that distance at which both impressions blend, than when proceeding in the reverse order, beginning at a smaller distance and gradually finding that distance at which the two separate sensations make their appearance; lastly, it becomes smaller the greater the attention and the greater the practice (hence it is generally smaller in blind people, Goltz); it is also said to become smaller by surrounding the skin with indifferent fluids (oil, water), having the same temperature as the body (Suslowa). Two impressions just felt distinct from each other

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Lastly, there are methods for determining at the same time the sensitiveness of cutaneous parts in a more extended sense, namely, by ascertaining the degree of perfection of our conclusions as to the configuration or the course of touching bodies. 1. The skin is touched with bodies of a definite configuration. 2. Different figures (letters) are drawn on the skin with a point, and the person experimented upon states in the first case the apparent figure of the touching body, and in the second that of the drawing.

In order to explain the above-stated facts relating to the reference of tactile impressions to space, the following assumptions are necessary (Lotze, E. H. Weber, Meissner, Czermak). We are continually conscious of the state of stimulation of all cutaneous points in their relation to space (our consciousness perceives a field of tactile sensation, as already stated). Every stimulation of a sensory end-organ is referred to a definite spot in the field of tactile sensibility, that is, on the surface of the skin. This spot is, however, not the *point* stimulated, but rather a circular or (on the extremities, p. 464) an oval *surface*, the centre of which is formed by the irritated point, the so-called *circle of sensibility* (see below). Two such circles, which either touch or partly cover each other, can, however, not be separately perceived; the separation takes place then only when between the two circles there is a *non-irritated sensory element* and the apparent distance of the two irritations is the greater the more numerous the non-irritated elements which remain between the two circles. From this it follows that two neighbouring impressions made on the skin can only be felt as separate when their distance is greater than the whole diameter of one circle of sensibility. The numbers given on page 464 are therefore the diameters of the circles of sensibility at the corresponding cutaneous places. It follows further, that two separate impressions blend when the intervening sensory elements are stimulated (compare the observation on p. 464).

There still remains to be explained how it is that these circles possess different sizes at the different parts of the skin. A circle of sensibility is evidently not an anatomical magnitude, such as the district of distribution of a nerve-fibre; for, firstly, it is altered by attention, practice, and other influences; and, secondly, it would be possible for the two feet of the compasses, if their distance were smaller than the diameter of one circle of sensation, in one case both to fall within one circle, in another case into two neighbouring circles (these being considered fixed). We must therefore assume the existence of a circle of sensation round each cutaneous point. To the above explanation is further to be added, that the circles are smaller the more closely packed the sensory organs; from which it follows that the assumption that the circle of sensation is caused by the mechanical effect of the irritation on a cutaneous surface, and not on a mere point (*circles of diffu-*

sion), is not enough: for if so, then the size of the circles would evidently be independent of the relative number of the end-organs, and therefore would in general be the same everywhere. It is rather to be assumed that the transmission of the irritation of one fibre to another sensory fibre in the neighbourhood is a central process (irradiation, associated sensation), and that it always extends from every point, in every direction, to the same number of sensory fibres (the distance of the two points of the compasses corresponds in the mean to twelve tactile corpuscles, Krause), but that by practice, attention, and acuteness of irritation, &c., it can be diminished. This view (see Chap. XI., under Spinal Cord) seems to correspond best with the observed facts.

Alterations in the normal amount of blood in the skin (hyperæmia, anæmia) diminish the tactile power (Alsberg); intense cooling of the skin (for instance, ether-spray) may produce complete anæsthesia; certain poisons brought in contact with the skin act in the same way.

Sensations of Temperature.

Sensations of temperature arise when the end-organs of sensory nerves are irritated by variations of temperature within the limits of about $+10^{\circ}$ to $+47^{\circ}$ C., particularly when the skin is either warmed or cooled by bodies in contact with it. The sensation caused by a positive variation we call sensation of warmth, that caused by the negative variation, sensation of cold. When the variation of temperature extends over a large surface, or over the whole body, then the sensation of cold changes to a sensation of shivering, and the sensation of warmth gives rise to a sense of heat. The symptoms mentioned at page 260 are connected with both (the shivering of fever is caused by the sudden cooling of the skin in consequence of the diminished flow of blood through the spasmodically contracted cutaneous arteries, whilst fever heat is due to the reverse process; in both, however, the mean bodily temperature is higher than normal). Variations of temperature between 27° and 33° C. are distinguished most acutely, then variations between 33° — 39° C., and then variations between 14° — 27° C. (Nothnagel). The different regions of the body may be grouped as regards their sensitiveness to changes of temperature (measured by the smallest yet perceptible variation) as follows (leaving out the extremities, which follow no law) (E. H. Weber): Tip of tongue, eyelids, cheeks, lips, neck, trunk. As the middle line is approached, the parts are less sensitive. The variation is felt more intensely the more rapid its occurrence, and the larger the affected cutaneous surfaces. Temperatures above or below the limit given above produce pain (p. 462). Variations are here no longer specifically felt.

Anæmia of the skin increases the sensitiveness for temperature; hyperæmia diminishes it (Alsberg).

If the principle of specific energies (compare p. 351) is to be a general one we must assume here, also, different fibres and different central organs for the tactile and temperature sensations; though we know nothing definite about this, it may be yet mentioned that the distances in the experiment cited on p. 464 are smaller when the temperature of the two points of the compasses differ (Czermak), and that in the experiments given on pp. 464 and 465 a colder weight is felt as heavier, so that the apparent difference of pressure becomes greater when the heavier weight is at the same time colder, and less when the lighter weight is colder, and that difference of pressure is felt with equal weights of unequal temperature (Weber).

Other Specific Sensations.

The sensory nerves of certain parts of the skin and mucous membrane of the genital organs (4th section), on being irritated, give rise to peculiar sensations, different from the tactile and temperature sensations, which are called *voluptuous sensations*.

We know very little about the specific sensations of those nerve-fibres which do not terminate in the skin. Some of these sensations, *hunger* and *thirst*, have already been considered (p. 227). There only remains for consideration—

The *muscular* sense (Weber). The presence of sensory fibres, though not anatomically demonstrated with certainty, is physiologically proved by the muscular pains observed under certain conditions, and by the *sense of fatigue* which undoubtedly occurs. The question is only whether these or other nerve-fibres explain to us the *state of activity* of the muscles. It is evident that many phenomena, such for instance as the combination of complicated muscular movements, depend on the intervention of centripetal fibres, for such movements become very defective when the posterior roots of the spinal nerves are divided (Bernard), or when the centripetally conducting parts of the spinal cord (see Chap. XI.) are injured or degenerated, for instance, in the grey degeneration of the posterior columns (locomotor ataxy). It is very improbable that these defects depend on the loss of cutaneous sensibility, for the movements are not at all, or very little, interfered with by skinning the animal (Bernard). It seems therefore that consciousness itself is aware of the condition of the muscles, &c. This may be brought about in the following ways:—1. Sensory nerves of the muscles give information about the changes in tension, pressure, and possibly also of the state of contraction. 2. Our consciousness judges of the voluntary impulse, which is imparted to the motor nerves, and of the effects which necessarily follow. 3. The sensorium is made aware of the effects of muscular activity by the surrounding parts (muscles, areolar tissue, &c.) Whether all these different ways, or one of them only, exists, is not known. The various uses of such a muscular sense are evident, partly from what has just been said (viz. co-ordination of movements, maintenance of equilibrium), and partly they are illustrated by facts

asly stated, as—estimation of weights lifted, knowledge as to the configuration of the surface of, and conclusions as to the nature of bodies touching.

The presence of sensory nerves in the *sartorius muscle* of the frog has lately been proved by the following facts:—1. After section of the anterior roots of the spinal nerves, the muscle contains non-degenerated nerve-fibres; and 2. In poisoning by strychnia, stimulation of the nerve to the gastrocnemius occasions no effect (Sachs). For facts concerning the mode of termination of sensory nerves of muscle consult p. 265.

2. The Perception of Motion.

Passive movements of the whole body, whether rectilinear or rotatory, are distinctly perceived even when the sense of sight is in abeyance; the power of perception soon disappears, however, if the movement be uniform. On suddenly arresting the movement there occurs the illusion that the body is moving in the reversed direction, so that possibly it is not velocity, but only acceleration, which is perceived (Mach¹).

■ Animals react towards *actual* as also towards the succeeding
■ apparent movements, especially in experiments on rotation, by
■ moving the body in the opposite direction (the eyes especially
■ refuse to participate in the movements, and follow intermittently,
■ 'Nystagmus'), so that during rotation the body is opposed to the
■ direction of rotation, but after its cessation tends in the same
■ direction as that of rotation. These movements occur involun-
■ tarily, and if the rotation be very rapid, they may degenerate into
■ rotatory spasms presenting a similarity to the 'uncontrollable
■ movements' described in Chap. XI. (Purkinje).

The sensitive mechanisms of all parts of the body appear sufficient to explain the perception of motion. As a result of every regular motion certain displacements of the more mobile parts of the body in reference to the less mobile must occur, owing to inertia, centrifugal force, &c.; the perception of these changes, no less than that of the altered pressure of the ground, of the surrounding medium, &c., and the perception of the muscular exertions necessary to maintain equilibrium, are sufficient to lead to unconscious conclusions concerning the kind, direction, &c., of the motion. That essentially acceleration is perceived, and that the succeeding rest appears as a negative acceleration, may be easily explained by the general principle of the greater sensitiveness to *changes* as contrasted with *states*. The supposition that a special sense-organ presides over the perception of motion is therefore superfluous.

It has recently been surmised that an example of such an organ is presented

¹ Mach, 'Versuche über den Gleichgewichtssinn.' (*Wien. Sitzungsbericht*, 1874.)
Grundlinien der Lehre von den Bewegungsempfindungen. Leipzig, 1876.

by the semicircular canals of the internal ear, after the injury of which a number of noteworthy phenomena have been observed (Flourens¹); the most constant of these is an oscillation of the head in the plane of the injured canal; the other phenomena, viz. an inclination to fall around an axis at right angles to the plane of the canal, uncontrollable movements around this axis, distortion of the head so that in the case of pigeons the beak is turned into the neck, &c.—may be altogether absent, or are only noticed after the animal has been irritated, or develop so late that they may be referred to a sympathetic affection of the contiguous cerebellum. Recent authors have drawn the conclusion from these phenomena that the semicircular canals constitute not an acoustic apparatus, but a definite sense-organ concerned in the perception of the absolute position of the head in space (Goltz), or in the perception of the movements of the head (Crum Brown,² Breuer, Mach), or that they discharge this function in addition to serving acoustical ends. Pressure, or the relative movements of the endolymph, is supposed to stimulate the nerve-terminations, and so rotations, decomposed by the three axes of the semicircular canals, are supposed to be perceived. The disturbances which are the results of injuries have been explained by some writers as due to the abeyance of the functions which control the position of the body in space, by others the occurrence of abnormal sensations of movements, as the so-called sensation of giddiness is referred to excitation of the organ.

It is surmised that in these organs are initiated the reflex acts which result in the previously-mentioned reactionary rotations, and that the dizziness accompanied by uncontrollable movements which follow the passage of a galvanic current through the head also take their origin in them. All these theories are controverted by the fact that after section of both nerves an animal does not lose the power of controlling its movements in space, and when subjected to passive movements or to the action of a current passed through the head, reacts as if uninjured (Cyon, Tomaszewitz). Moreover, persons who are destitute of a labyrinth exhibit no other abnormality but deafness; besides which, the acoustic function of the semicircular canals is conclusively proved by anatomical considerations (the semicircular canals are as closely connected with the utricle, as is the ductus cochlearis with the saccule, and in the lower vertebrates the former constitutes the chief organ of hearing).

The pendulum-like movement observed by Flourens is perhaps explained by disturbing sounds which the animal hears in a particular direction, it being surmised that the direction of the semicircular canals has something to do with the perception of the direction of sound.

[*The Perception of the Position of the Body in Space.*—Cyon³ has very recently published an experimental investigation which has led him to reject entirely the hypotheses of Mach, Crum Brown, and Breuer, and to develop the theory that the semicircular canals are the peripheral organs of the *sense of space*, i.e. that sensations originating in the stimulation of the nervous end-organs in the ampullæ lead to the formation of our conceptions of the three dimensions of space. The sensations originating in each canal correspond to one of these dimensions. By the aid of these sensations there may be formed in our brain a conception of an ideal space to which will be referred all the perceptions of the other senses which relate to the position of the bodies which surround us, and the position of our own body in relation to them.

The experiments of Cyon have led him to reject the view which had been advanced by Goltz and accepted by Mach, Crum Brown, and Breuer, viz. that

¹ Flourens, *Recherches expérimentales sur les propriétés du système nerveux*. 1842.

² Crum Brown, 'On the Sense of Rotation and the Anatomy and Physiology of the Semicircular Canals of the Internal Ear.' *Proceedings of the Royal Society of Edinburgh*, Jan. 19, 1874, and *Journal of Anat. and Phys.*, vol. viii. (1874), p. 327.

³ *Recherches expérimentales sur les Fonctions des Canaux semi-circulaires et sur leur rôle dans la formation de la notion de l'espace*. Thèse pour le Doctorat en Médecine présentée et soutenue le 1^{er} Avril, 1878, par Elie de Cyon. Paris, 1878.

the endolymph being set in motion is the agent in exciting the end-organs of the nerves of the ampullæ; he rather believes that the agitation of the otoliths and of the epithelial processes of the ampullæ, either by movement of the head or by waves propagated through the endolymph, is the proximate cause of the stimulation of the ampullary nerves. The stimulation of the end-organs of any one semicircular canal would produce, according to Cyon's theory, a sensation of extension in a plane perpendicular to the planes of the two other canals, and the excitation of the three canals would furnish us with a sensation of extension in three planes at right angles to one another; and these unconscious sensations would lead to the formation of our conception of space of three dimensions.

Cyon is led, in the development of his theory, to reject the auditory functions of the vestibular branch of the auditory nerve. According to him the eighth pair is composed of the auditory nerve and of a 'nerve of space.' He is inclined to deny the auditory function of the vestibule and semicircular canals in the lower organisms. Such organisms would, according to Cyon, possess an organ of the sense of space, quite essential to all animals possessing the power of locomotion, but no organ of hearing.]

CHAPTER XI.

THE CENTRAL END-ORGANS OF NERVES (CENTRAL NERVOUS ORGANS).

A. GENERAL CONSIDERATIONS.

THE central end-organs of nerve-fibres are contained in certain structures which are called the 'central organs of the nervous system.' The latter contain, in addition to the central end-organs, numerous conducting fibres. Their function is, therefore, much complicated by the fact that they are able to act also as conducting agents. Since the investigation of the central nervous end-organs has never, hitherto, been possible apart from the nerve-fibres with which they are mixed, a physiological consideration of them is not possible in the present state of our knowledge. We can, therefore, only adduce the discoveries which have been made concerning the functions of the mixed organs—brain, spinal cord, and ganglia—to serve as material for the future physiology of the nervous end-organs which have not yet been isolated.

All organs of the body which can be shown to possess the above characteristics contain as necessary constituents *ganglion-cells*, which are immediately in communication with nerve-fibres, and which are therefore considered to be the essential elementary structures of nerve centres (or at least analogous cellular arrangements). This surmise is the more probable as ganglion-cells can be discovered in most automatically acting organs. On the other hand, central functions have not been discovered to belong to all nerve-cells. Concerning the physiological properties of ganglion-cells almost nothing is known. The nature of their chemical composition can only be imperfectly and approximately gathered from analyses of the grey substance of the brain. The white substance of the brain, which consists essentially of nerve-fibres and a connecting substance (neuroglia), is considered to be of the same composition as nerve-trunks; the constituents of the latter, indeed, have been chiefly determined by examinations of brain and spinal cord. While the reaction to test-paper of the white substance is neutral or alkaline, the grey substance has been found to be acid (Gscheidlen), a circumstance which is probably to be attributed to the rapid changes occurring at the surface of section. The chemical constituents of the white substance are cerebrin, lecithin, and pro-

bably compounds of lecithin; albumin, potassium-albuminate and globulins; neurokeratin; cholesterin and fats; creatine, xanthine, and hypoxanthine; inosite and some anhydride of sugar; lactic acid (the ordinary modification according to Gscheidlen) and volatile fatty acids; salts and water. The grey substance of the brain is distinguished chemically from the white chiefly by containing more water, albumin, lecithin, and lactic acid, and less cholesterin, fat, and protagon.

A considerable number of substances which are now known to be either the products of the decomposition of lecithin, or the mixtures of such products with other bodies, were formerly described as genuine constituents of brain substance. Even the above-mentioned constituents may be themselves the results of the decomposition of more complicated pre-existing compounds. One of them, protagon, has recently been regarded as a mixture of lecithin and a nitrogenous glucoside, cerebrin (Hoppe-Seyler), a body which chiefly occurs in the white substance (Petrowsky). The composition of grey and white brain-substance is given in the following table (Petrowsky):

						Grey substance.	White substance.
Water						81·6 p.c.	68·4 p.c.
Solids						18·4	31·6
Consisting of							
Albumins and gelatin						55·4 p.c.	24·7 p.c.
Lecithin						17·2	9·9
Cholesterin and fats						18·7	51·9
Cerebrin						0·5	9·5
Substances insoluble in ether						6·7	3·3
Salts						1·5	0·6

It is in the highest degree probable that processes of oxidation take place in ganglion-cells as in all other organs. It is, however, still but a probability, unless we consider it evidenced by the fact that the venous blood of the brain and spinal cord is as poor in oxygen and as rich in carbonic acid (*i.e.* as dark in colour), as the venous blood of any other region of the body. We are equally ignorant as to whether such processes of oxidation are concerned in the activity of the ganglion-cells, and, if so, to what extent; we cannot say whether that activity is not dependent upon processes of decomposition similar to those which occur in muscles and nerves; or what are the results of such oxidations or decompositions.

Whether we ought to add to the general properties of the ganglion-cells that of irritability, when acted on by the common nervous stimuli, is not yet decided. Certain experiments on the non-irritability of the spinal cord under mechanical stimulation, which will be discussed hereafter, indicate that ganglion-cells differ from nerves in this respect, probably to a considerable extent. For certain nerve-cells particularly, certain stimuli are known which differ from the general nerve-stimuli, *e.g.* many of the motor centres of the *medulla oblongata* and of the spinal cord are excited by the blood of dyspnoea.

Finally, ganglion-cells possess a certain *periodicity* in their

activity. This is exemplified by periodic automatism. But, in addition, any tetanic stimulation of the spinal cord calls forth a periodic excitation of the motor cells, which recurs 19·5 times per second, and which is quite independent of the number of stimulations acting on the cord. In the study of sensory structures it has also been ascertained that luminous stimuli affect the central organs connected with the optic nerve most strongly when they follow one another 17 or 18 times in the second; and, similarly, stimulation of the auditory nerve is most efficient when intermit- tences occur 33 times in the second. Perhaps stimulations of these particular frequencies are most efficient because they coincide with the imminent periodicity of the ganglion-cells (just as a resonator is most strongly excited by its own proper tone).

General Functions of the Central Organs.

As was stated in the Introduction, the following are the characteristic functions of the central organs of the nervous system:

1. Reflex acts or reflexes, *i.e.* transmission of the effects of stimulation from afferent to efferent fibres;
2. Automatic acts, *i.e.* the property of independently stimulating efferent fibres;
3. Psychical functions.

It was formerly supposed that *reflex actions* necessitated special (excito-motor) nerve-fibres, which proceeded from sensory end-organs to a central organ, there to change their direction and to become efferent. This hypothesis, which involved the existence of a special nervous system exclusively devoted to reflex acts, and which did not at all explain why the change in direction of the fibre did not occur at any part, even outside, of a central organ, is destroyed by the fact that an afferent fibre does not always liberate the same, but on the contrary the most varied, reflexes, and may even excite in a reflex manner *all* efferent fibres. Similarly, the conception that reflexes depended upon deficient insulation of afferent and efferent paths in the central organs had to be given up, because of the regularity and functional importance of these acts. The now general supposition that reflex acts depend upon the anatomical connections between fibres belonging to sensory and motor paths is not free from serious difficulties, inasmuch as the effect of stimulation does not always travel along a certain beaten track, but, under the influence of suddenly arising conditions, chooses at one moment one, the next moment another, way. It would appear that this selection of paths depends partly upon the meeting of centripetal stimulations, partly also on the influence of special directing nerves which abut at the points of intercommunication of the nerve-fibres.

As *automatic* acts are classed all those acts of central organs which have not been shown to originate through the intermedia-

tion of any liberating agent. In many cases, however, the existence of such an agent is surmised, and an attempt is made to include apparently automatic actions under the class of reflex acts (consult in reference to this, at p. 201, the liberation of respiratory movements, and the section on the 'muscular tone'). Where no liberating force is present, the proximate causes of the excitation must be sought for in the exchanges of matter which are going on in the nerve centre. These exchanges may very well be associated with continuous transformation of energy, leading to an excitation of the origin of the nerves. Automatic stimulations are in great part periodic, and even those which are *tonic* or *tetanic* in their nature, may be classed as periodic in character (p. 274). The occurrence of periodic excitation may be conceived in various ways, *e.g.* by surmising a resistance which can only be overcome when the liberated energy has attained a certain intensity; very much as a gas which is being continuously generated, but has to pass through water, is discharged through it in rhythmically succeeding bubbles. Even a very quickly ensuing exhaustion might explain the resistance referred to in the last paragraph.

Many automatically-acting centres are under the control of *regulating nerves*, which in some cases merely affect the duration of the periods (*i.e.* the frequency), in others the intensity of the excitations, whilst in the third class of cases they exert an influence upon both. To the first category belong the *accelerating* and *retarding*, to the second the *exciting* and *inhibitory* nerves. It is only in the case of the latter that there can be any question as to *automatism* (compare the section on vaso-constrictor and vasodilator nerves, p. 111). In the case of periodic automatic actions it occurs that acceleration is associated with a diminution of intensity, whilst retardation is associated with intensification, so that, in truth, as is instanced in the case of the influence exerted by the vagus on respiration, the total activity remains the same (Rosenthal, compare p. 201). In this case, the action of regulating nerves may be conceived as only increasing or diminishing the previously mentioned resistance without exerting any influence upon the amount of activity; in the example of the gas-bubbles the action of retarding valves would be simulated by increasing the consistence of the fluid, which would cause the bubbles to be larger but less frequent, and the action of accelerating nerves by diminishing the consistence, when the bubbles would become more frequent and smaller. It is clear that a progressively increasing diminution of resistance would in the case under consideration ultimately lead to *tetanus*, whilst a progressively increasing resistance would lead to the suppression of excitation, the retarding nerve then assuming the position of an inhibitory nerve. Still there are some cases (*e.g.* that illustrated by the action of the vagus on the heart, Ludwig and Coates, p. 109) in which the activity is

in no ways constant, so that even in the case of periodic automatism there are regulating nerves which directly influence the amount of excitation, as is indeed always the case with tonic automatism.

Of *psychical* processes only those absolutely require physiological consideration which are in immediate relation with afferent and efferent nerve-excitations, viz. *sensation* and *will*. Unless one is willing to admit the inadmissible assumption that processes which are not essentially movements of material particles are able to occasion movements in material particles, and the converse, we are compelled to surmise the existence of a connection between the nerve-excitations connected with sensation and with will, which is analogous to reflex actions.

This subject will be further discussed in connection with the physiology of the cerebral hemispheres.

SPECIAL PHYSIOLOGY OF THE CENTRAL NERVOUS ORGANS.

There must now be described whatsoever has been discovered concerning the functions, as centres and as conductors, of the various central organs, viz. brain, spinal cord, and sympathetic ganglia. It must be expressly borne in mind that only those facts which have been established with some degree of certainty will be noticed in this, the darkest, region of physiology.

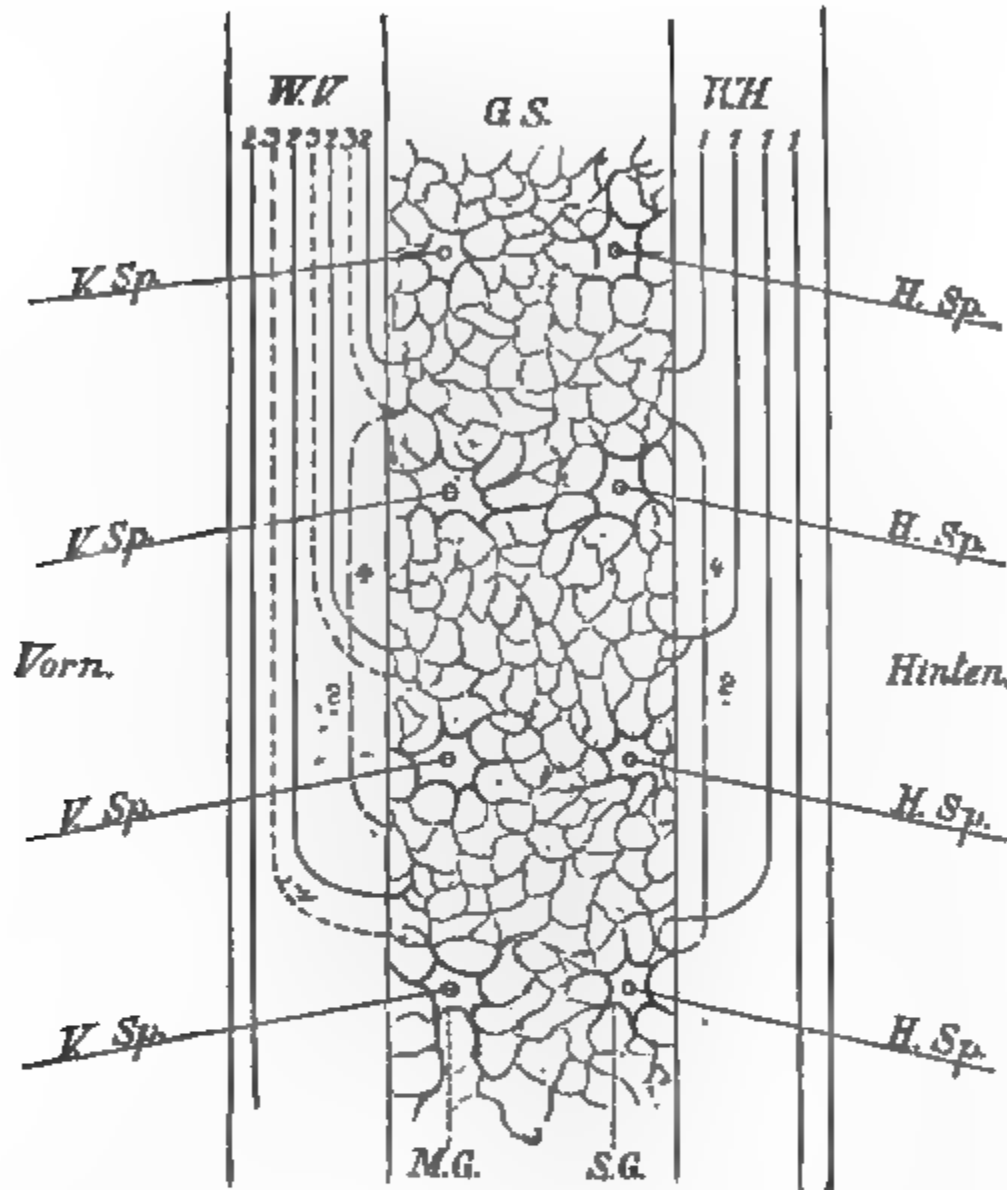
1. Spinal Cord.

STRUCTURE.—The most important points, physiologically, in the structure of the spinal cord are the following:—In a cross section of the cord there are distinguished, 1. The narrow central canal lined by epithelium. 2. The grey substance which surrounds that canal, and projects in the form of horns (anterior and posterior cornua) into the white substance. 3. The white substance, in which one may distinguish on either side of the median fissures, three columns, the anterior, lateral, and posterior; between the anterior and lateral columns lie the anterior cornua of the grey substance, and the fibres of the anterior root of the spinal nerve which enter it. In like manner the posterior cornua and the fibres of the posterior root lie between the posterior and lateral columns. The white substance, besides the root fibres traversing it in an horizontal direction, consists of vertical (longitudinal) fibres and a connecting substance (neuroglia). The grey substance consists of ganglion-cells, and a homogeneous grey mass, in which the majority of recent observers describe an interlacement of fine axis cylinders running in all directions.

The ganglion-cells lie for the most part in the anterior and posterior cornua. There is distinguished in every ganglion-cell (Deiters) a granular mass (protoplasm), a large nucleus with nucleoli and processes. Among the processes one—the axis cylinder, which, as it seems, is in connection with the nucleus—may be at once detected by its appearance; the remaining processes are fine, numerously branched, pointed fibres (processes of protoplasm), into which

homogeneous fine simple fibres—axis cylinders of the second kind—are inserted. The latter join the fine network of fibres of which the main mass of the grey substance consists (Gerlach), and from which fibres, united so as to form thicker bundles, run into the white substance. According to recent theories (M.

FIG. 68.



G.S. grey substance, W.V. white anterior column, W.H. white posterior column, V.sp. anterior root-fibres, and H.sp. posterior root-fibres, of spinal nerves. M.G. motor ganglion-cell of grey anterior cornu, S.G. sensory ganglion-cell (?) of grey posterior cornu, 1 1 1 1 sensory fibres, 2 2 motor fibres, 3 inhibitory fibres, 4 4 co-ordinating fibres (?)

Schultze), the cells consist of a fine fibrillar network, the processes also being fibrillated; if so, the cells are merely traversed by the fibrillae of the processes.

The large axis cylinders (those of the first kind) are the terminations of the root-fibres of the spinal nerves. The cells into which the fibres of the anterior root enter ('motor ganglion-cells') are larger and have more numerous protoplasmic processes than the more spindle-shaped cells into which the posterior root-fibres enter ('sensory ganglion-cells'). According to another view (Gerlach), the fibres of the posterior roots do not in general enter into ganglion-cells, but pass directly into the fibrillar network of the grey substance, so that the cells of the posterior cornua also are probably to be reckoned as motor.

The course of the fibres in the spinal cord, the investigation of which has by the introduction of new methods (study of their rudiments in the embryo,

Flechsig¹) entered upon a new epoch, cannot properly be considered in this work.

It is clear from the anatomical arrangement of the parts that the spinal cord is, with the exception of the thin sympathetic communications, the only connection between the brain and the nerves of the trunk and extremities. The spinal cord must therefore contain the paths for the conduction of all voluntary movements of the trunk and extremities, for all sensations in those parts, and for all actions not psychical of other cranial centra (e.g. the respiratory centre).

It is, however, established on anatomical grounds that the nerves of the trunk in the spinal cord do not simply run to the brain, but that all of them, or at least the motor nerves, are first of all connected with ganglion-cells. Moreover, there are physiological reasons against the view of the direct entrance of the nerves of the trunk into the brain, as will be seen on consulting the sections on Reflex Actions.

No well-ascertained anatomical facts have, as yet, been discovered which throw light on the conduction of impressions from motor and sensory ganglion cells to the brain. It is most probable that the cells are immediately connected with a complicated network of fibres, which continues uninterruptedly to the brain, but from which fibres continually separate and run to the brain isolated in the white substance. In order to understand the matter, it is necessary to assume that impressions only travel along structurally continuous paths—paths morphologically pre-existent—but that they are able to pass along those paths in every direction where continuity of the conducting structure is established. According to this supposition a nervous impression, when once it has gained the actual, anatomical, network of fibres, may pass along every individual fibre which is fitted for conduction.

The result of an excitation of a sensory fibre of the trunk or extremities is either a *Sensation*, which is referred with more or less exactness to the peripheral termination of the fibre, or a *Reflex Action*, i.e. an excitation of a motor fibre without the aid of consciousness, i.e. an excitation which is involuntary.

Reflex Functions of the Spinal Cord.

REFLEX ACTS following excitation of the same sensory fibre may be of the most varied kinds. Individual muscles may contract, whereby regular, and, in a certain sense, purpose-like movements may be produced; or apparently disorderly movements may result, in more or less limited muscular regions, or in all the muscles of the body.

¹ Flechsig, *Die Leitungsbahnen im Gehirn und Rückenmark des Menschen, auf Grund entwicklungsgeschichtlicher Untersuchungen dargestellt.* Leipzig, 1876.

ORDERLY REFLEX MOVEMENTS may be best observed in animals the mental organs of which have been removed by separation of the brain from the spinal cord; and, for the latter operation, frogs are the most convenient. Beheaded frogs, when stimulated, make regular and purpose-like movements of defence, which differ so little from voluntary movements having the same object that some have ascribed them to mental organs situated in the spinal cord (Pflüger¹). Orderly reflex acts have not all a defensive character, many purposive reflex processes having other objects. Thus the following phenomena may be observed in frogs whose cerebra have been separated from their spinal cords (Goltz²):—1. That they croak regularly when the skin in the neighbourhood of the back is gently stroked, or when the nerves supplying that skin are mechanically irritated. 2. That, during the breeding season, the male will clasp the female firmly and continuously if the back of the latter be applied to the breast of the former, or if any other similarly-shaped structure, such as the finger of the experimenter or the back of a male frog, be similarly applied. On the other hand, an uninjured frog does not croak regularly on having its back stroked, and will only clasp an object as it is accustomed to clasp the female if copulation have been interrupted immediately before (Goltz). The consideration of these differences will be resumed hereafter.

Even in mammals the orderly reflex functions of the isolated spinal cord may be observed, *e.g.* by killing the brain by ligaturing its four principal arteries (S. Mayer, Luchsinger), or by cutting through the middle of the spinal cord and observing only the parts attached to the lumbar portion of the cord (Goltz). Very young animals also exhibit the same reflex acts as frogs when they are beheaded. Amongst the orderly reflex actions connected with the lumbar portion of the spinal cord are to be mentioned (Goltz with Freusberg and Gergens³): scratching regions of the skin which are tickled; discharge of urine when the bladder is full, especially upon irritation of the anus; also erection of the penis when it is stimulated; all the reflex acts requisite for coitus, as well as for gestation and parturition; and the reflex acts connected with the vascular system.

In man the orderly defensive movements which occur during sleep are in great part purely spinal reflexes, as, at any rate, mental organs are eliminated; the same may be said of many unconscious needful acts which are performed in the waking condition.

A beheaded, or brainless, frog, will take up a sitting posture like the uninjured animal; if pinched with forceps, it will press with the feet against the instrument in order to push it away; if a drop of acid be placed upon the skin,

¹ Pflüger, *Die sensorische Function des Rückenmarks*. Berlin, 1858.

² Goltz, *Functionen d. Nervencentren des Frosches*. 1869.

³ Goltz, 'Ueber gefässerweiternde Nerven.' *Zweite Abhandlung*. Pflüger's *Archiv*, vol. xi. p. 52.

it whisks it off at once with its feet, &c. These protective movements are very regular, but they admit of variations. If, for instance, that leg be cut off which is employed under ordinary circumstances in the removal of an irritant from a certain spot of skin, another limb will be brought into play, after some ineffectual movements of the stump, for the accomplishment of the same object. In this case the stimulus is not indeed the usual one; but it has had time, during the vain attempts of the frog to remove the irritant by means of the stump, to reach such an intensity that a mechanical explanation of the phenomenon is still possible.

For the performance of orderly reflex acts that portion of the cord with which the implicated sensory and motor nerves are directly connected is all that is necessary. For example, the second experiment above detailed may be shown with only that portion of the trunk bearing the anterior extremities, viz. with the portion of the back between the skull and the fourth vertebra, and the attached shoulder-girdle and arms.

Besides orderly reflex movements, movements of a disorderly nature, without any definite object, may occur; such movements are described as *reflex convulsions*. They only take place under abnormal conditions, as, for example, on very powerful stimulation, or after the operation of certain poisons (strychnia), or of certain pathological processes (traumatic and rheumatic tetanus, hydrophobia). They consist of transitory tetanic contractions of single groups of muscles, or of all the muscles of the body, on the application of a sensory stimulus. The less developed the abnormal condition of the spinal cord is, the more limited are the convulsions, and the stronger is the stimulus necessary to induce them. When, owing to an increased development in the abnormal condition, or to an increase in the strength of the stimulus (the stimulus being supposed to be applied to a limited portion of the skin), the reflex convulsions extend over a wider and wider area, they take the following course (Pflüger):—They are first manifest in the muscles, the motor fibres of which arise in the cord on the same side and at the same level; then they spread to the muscles supplied by the fibres of the opposite side, but still only to those which are symmetrical with the muscles of the side first affected, and they are never more intense in the latter than in the former; afterwards the convulsions affect muscles supplied by fibres given off at levels which are nearer and nearer to that of the medulla oblongata; and, finally, the muscles supplied by all fibres enter into general tetanic convulsions, which, owing to the superior strength of the extensors, give rise to the appearance known as *stretching convulsions*. The fibres proceeding from the medulla oblongata may, without any such great extension of the reflex processes, be implicated in convulsions of a reflex nature, as will be shown below.

In poisoning by strychnia, the slightest disturbance of the patient, such as by a draught of air or a vibration of the couch, is enough to induce a paroxysm. It has recently been observed that, during the condition of apnoea, the reflex convulsions characteristic of strychnia and similar poisons do not occur (Rosenthal and Leube, Uspensky); according to Buckheim this result follows all passive movements.

In order to understand reflex activity, it is necessary to suppose a union of motor and sensory ganglion-cells, and, moreover, a union in manifold ways. As direct anastomoses of these cells do not occur (Deiters), this union can only be effected by means of the above-mentioned grey network of fibres. But since this network apparently unites all the ganglion-cells of the spinal cord together, while it is certainly possible to understand the extension of the reflex process to all the muscles of the body, as occurs in the general convulsions of strychnine poisoning, it is as difficult to see how the reflex process is ever limited and localised, or how it results in orderly acts, as it is to understand the isolated conduction of sensations to the brain, or the voluntary production of isolated movements in the trunk.

In order, therefore, to reconcile the physiological possibilities with the anatomical facts, it is necessary to assume that under ordinary circumstances there exists throughout the network of fibres a very great resistance to conduction, so that the excitation or impression, even at a short distance from the sensory cell, which had been directly stimulated, becomes reduced to an almost imperceptible strength. In consequence, excitation can only be distributed (*a*) in the neighbourhood of the stimulated cell, causing limited reflex actions, (*b*) along paths where conductivity is more perfect, and which do not originate in the fibrous network at too great a distance from the point of stimulation. Such paths of more perfect conductivity are, apparently, the fibres which were described as emerging from the network and running in the white substance to the brain. In this way the isolated conduction of sensibility, as well as that of voluntary impulses to movement, become intelligible (compare fig. 68, p. 477).

The production of orderly, purpose-like reflex movements remains unexplained on this theory, since it is not certain that, in such movements, the impressions are transferred to the motor cells in the immediate vicinity. It must at least be first shown that the situation of the cells is such that the motor cells respond to the stimulation of the sensory cells nearest them by the most perfect movements for the purposes of defence, an arrangement which is, of course, quite possible. It is, however, quite as probable that, by an inherited perfection of organization, conduction from every sensory cell in the network is especially favoured in certain directions (by a diminution of resistance in those directions), whereby purpose-like movements are subserved or that combinations are formed, more readily capable of conducting, by means of the fibres of the white substance.

The abnormal extension of the reflex process, first of all to neighbouring motor cells, then to motor cells more remote, and finally to the whole number of them, would further be explained by supposing a diminution of the above-mentioned resistance to

conduction, which strychnia and the pathological causes of tetanus might be able to bring about in an extraordinary degree. If this were the true explanation, the power of referring sensations to definite localities, and of producing, voluntarily, local movements, would also be prejudiced; but concerning this we have no exact information.

This hypothesis admits, on the other hand, the possibility of the existence of influences capable of increasing the resistance to conduction, and therefore, of (1) rendering more difficult the production of reflex acts, and (2) rendering keener the powers of localising sensations and voluntary movements; and such influences have in fact been demonstrated.

INHIBITION OF REFLEX ACTIONS occurs chiefly through the influence of the will. All orderly reflex acts, such as have been previously described, occur with regularity only during sleep or after removal of the cerebrum. Under the influence of the will they are just as often suppressed as permitted, as is evidenced by the following examples: the refraining from scratching an itching part, or from emptying the bladder when the desire to do so exists, or from closing the lids when the eye is touched; and analogous phenomena occur even in the operations of the brain. Voluntary inhibition of reflex acts extends, however, only to such movements as may be originated by the will without any stimulation of sensory nerves; thus, neither can ejaculation of semen be voluntarily induced, nor can the reflex act once provoked be suppressed.

A second order of reflex inhibitions are such as are provoked by the strong stimulation of any sensory nerve, actually even by the strong stimulation of the very afferent nerves which occasion the act (Goltz, Setschenow, Nothnagel, Lewisson, Fick and Erlenmeyer).

Lastly, a third order of reflex inhibitions depends upon the activity of peculiar inhibitory apparatuses existing in the brain, which are, however, distinct from the mental organs; in the frog these inhibitory centres lie in the optic lobes (Setschenow¹). Section of the cord occasions, in consequence, an increase in the reflex excitability in the region of the cord below the section, which bears some resemblance to the conditions induced by poisoning with strychnia, conditions formerly known as 'hyperæsthesia' and 'hyperkinesia,' and peculiarly evident, by comparison, if one-half only of the cord be divided. The changes which are produced in this way must, in part, be ascribed to a stimulation of the reflex mechanisms originating at the divided part, so that it cannot be said that a tonic inhibition of the reflex mechanisms by the inhibitory centres has been rigidly proved (Herzen, Setschenow and Paschutin). Stimulation of the inhibitory centres prevents reflex acts.

¹ Setschenow, *Ueber die Hemmungsmechanismen für die Reflexthätigkeit des Rückenmarks*. 1863.

The customary way of measuring reflex excitability in frogs is (Türck) to immerse the leg in dilute acid, and to determine with the metronome the time when the leg is withdrawn from the acid. This time is not to be mistaken for the reflex-time; it is much rather the time required for the acid so to attack the skin as to excite a reflex act; nevertheless, the longer the interval between immersion and withdrawal of the leg, the smaller the reflex excitability of the cord. The time is increased by stimulating, either by means of powdered salt or of blood, the optic lobes, both salt and blood acting as stimuli to the inhibitory centres (Setschenow).

According to some there exist certain poisons which depress reflex excitability, and which do so by stimulating those centres which, it is believed, are also stimulated by the condition of the blood which exists in dyspnoea (Weil).

The reflex inhibitions now under discussion differ from the voluntary reflex inhibitions, inasmuch as the former affect all reflex acts, the latter only certain of them. According to a recent investigation of Ludwig and Woroschiloff,¹ there exist also centripetal fibres which are in a state of tonic excitation, and which inhibit reflex acts.

It has recently been sought to classify reflex acts according to the method of their liberation (Setschenow, Danilewsky). Those induced by means of touching are called 'tactile reflex movements,' to distinguish them from 'pathic reflex movements,' or such as follow the chemical or otherwise destructive and painful irritation of the skin. These two sorts of inducing, or liberating, impressions have, moreover, been thought to travel along different centripetal paths, since the reflex movements induced by them differ in their nature. Such a distinction—which may possibly be supported on anatomical grounds—would, at the same time, explain the difference which exists in the power of the mind to refer to their exact locality impressions of a tactile and of a painful nature, the former being localised by the mind with far more exactness than the latter, which appear to radiate or extend over a considerable surface beyond the point of application of the irritant. (This difference may, however, be explained in the manner given on p. 489.) It would appear, further, that it is only reflex movements of a 'pathic' nature which are capable of inhibition by means of Setschenow's centres; while 'tactile' reflex movements, on the other hand, can only be inhibited by means of the will. These differences will be again spoken of.

There is yet no theory which satisfactorily accounts for the facts of reflex inhibition. Inhibition by the will might be conceived to be due to fibres of the anterior columns entering the grey matter and reinforcing the previously-mentioned resistance to conduction in the regions around their points of entrance (such fibres have been represented by 3 3 in fig. 68, p. 477); yet such an action is not comprehensible. Many thinkers regard all reflex inhibitions, especially such as are induced by the strong stimulation of sensory nerves, as due to a kind of interference-action, which, however, is also scarcely comprehensible.

The following facts have been observed in reference to spinal reflexes; the condition of apnoea appears able to suppress them (Rosenthal, compare p. 480). Individual stimuli only induce reflexes when they are very powerful, whilst rhythmical stimuli applied to the skin (induction shocks) act the more quickly and powerfully the more frequently the individual stimuli succeed; so that we must surmise that a summation or addition of centripetal

¹ Ludwig u. Woroschiloff, 'Der Verlauf der motorischen und sensiblen Bahnen durch das Lendenmark des Kaninchen.' *Ludwig's Arbeiten*, 1874.

excitations occurs in the central organ, and indeed it is doubtful whether a single stimulus can excite a reflex act at all (Ludwig and Stirling,¹ Rosenthal).

The time occupied by a reflex act (*reflex-time*) may be measured by determining in brainless animals the time intervening between stimulation and movement; the time occupied in conduction by the nerves, as well as the latent period of muscular contraction, being determined in separate experiments. Fresh determinations (Helmholtz, Rosenthal,² Exner,³ Wundt and others) have given as the value of the reflex time $\frac{1}{20}$ th of a second or even less; the reflex time is lengthened by cold, and shortened when the strength of the stimulus is increased, as well as by strychnia. Further, the time is longer when the nerves concerned in the reflex are not at the same spinal level, and especially is it lengthened when the effect has to cross the spinal cord.

According to a recent work (Ludwig and Owsjannikow⁴) orderly reflexes occur between very different spinal levels, e.g. between the hind and fore extremity, and conversely—not, however, when the medulla oblongata is separated—so that within the latter must be situated a reflex central organ of a higher order which can bring into communication different spinal levels by means of white longitudinal fibres; nevertheless, the general diffusion of reflexes which strychnia brings on, occurs even in the isolated spinal cord.

Other Functions of the Spinal Cord.

From what has preceded it follows that the chief importance of the spinal cord lies in the fact that its grey matter contains the immediate centres for all the efferent nerves of the trunk, which can be thrown into reflex activity by centripetal nerves, especially by those which join the cord at the same level (these centres may therefore be called 'Niveau-centres'). The reflexes occasioned in this way offer the first example of animal reaction, and under normal circumstances are sufficient for the preservation of the organism. By the interlocking of reflex apparatuses of a higher order, and by the addition of mental organs, the reaction of the animal becomes more developed and better suited to the circumstances of the environment, though the reflexes *in one plane* become also more restrained.

The efferent nerves of the spinal cord govern the movements of the whole trunk and its extremities, the movements of the

¹ Ludwig u. Stirling, 'Ueber die Innervation elektrischer Hautreize. Ludwig's *Arbeiten*, 1874.

² Rosenthal, 'Untersuchungen über Reflexe.' *Sitzungsber. d. Physik. Med. Soc. in Erlangen*. 1878.

³ Exner, *Experimentelle Untersuchung der einfachsten psychischen Prozesse*. Zweite Abhandlung. 'Ueber Reflexzeit und Rückenmarksleitung.' *Pflüger's Archiv*. Vol. viii. p. 526.

⁴ Ludwig u. Owsjannikow, 'Ueber einen Unterschied in den reflectorischen Leistungen des verlängerten und des Rückenmarkes der Kaninchen.' Ludwig's *Arbeiten*, 1874.

viscera, the constriction and dilatation of the vessels, except in the case of the head and many secreting glands. For many of these organs the *spinal level* ('*Markniveau*') is known; thus, for the vessels of the head, for the *dilatator iridis*, for the smooth muscles of the eye-ball (muscles of Müller), perhaps also for the secretory fibres of the cervical sympathetic (saliva, tears), the centre is situated on the borders between the cervical and the dorsal spinal cord (*Regio oculo-spinalis, centrum ciliospinale*, Budge), whence the fibres concerned proceed out of the spinal cord, passing through the anterior roots of the spinal nerves into the course of the cervical sympathetic. For the uro-genital and rectal apparatus the centre lies in the lumbar portion of the spinal cord, *e.g.* for the *sphincter ani* the centre lies, in the dog, at the lower third of the fifth lumbar vertebra (Budge, Giannuzzi, Masius), in the rabbit the centre lies between the sixth and seventh lumbar vertebræ (Masius); the centre connected with the closure of the bladder lies immediately beneath the preceding (Masius).

Besides being influenced by *reflexes in one plane* and by the action of parts of the brain, these spinal centres are also directly excited by many conditions, as by the dyspnœic condition of the blood, by heat, poisons, &c. Whether in these cases automatic excitation occurs, is doubtful. The usual automatic actions which appear to depend upon them are either in reality reflexes—as, for instance, the tone of the sphincters—or they have their origin in higher centres; such is the case with the tonus of the *dilatator iridis* and the vascular *tonus*. Nevertheless, after section of the spinal cord, the vascular tonus of the posterior parts of the body is observed to be reestablished after some time, and only disappears altogether after destruction of the posterior segment of the cord (Legallois, Goltz,¹ Vulpian); so that a species of vicarious tonic automatism is set up (a similar and further process occurs after destruction of the spinal cord, through the agency of the peripheral ganglia in connection with blood vessels). Another very doubtful automatism is that of Muscular Tonus.

The Tonus of Muscles.—By '*muscular tonus*' is understood a constant, slight, and involuntary contraction of all the muscles of the body, but especially of those of animal life, which is dependent upon the nervous system. All the appearances which are usually received as proof of the existence of this constant tonus are, however, capable of explanation in other ways. Thus, the retraction of severed muscles, which was supposed to be due to it, takes place when the nerves supplying the muscles have been previously divided, and is merely due to the fact that muscles in the body are extended somewhat beyond their natural length. Again, distortion of the face after paralysis of the facial nerve on

¹ Goltz, 'Ueber die Functionen des Lendenmarks des Hundes.' Pflüger's *Archiv*, vol. viii.

one side need not depend upon a deficiency of muscular tonus on that side, but upon the fact that, after contraction of the muscles of the opposite side has once occurred, there is no means of re-extending the muscles to their original shape. But the assumption of any such real automatic tonus may be directly disproved by first of all making a preparation in which an extended muscle is still connected with its motor nerve and the central nervous system, and then dividing the nerve, when it will be noticed that the muscle does not become in the slightest degree elongated (Auerbach, Heidenhain).

On the other hand, individual voluntary muscles may, under certain conditions, be shown to be under an involuntary and weak contraction, which is not, however, automatic, but reflex in its nature. If a frog be vertically suspended, after having its brain separated from its spinal cord, and the nerves of one of its hinder legs be divided, it will be noticed that the injured leg hangs more loosely than the uninjured one. The same results follow if, instead of dividing the whole sciatic plexus of nerves, the posterior roots alone be cut. Hence it must be concluded that the slight flexion of the uninjured limb is not due to an automatic, but to a reflex action which is liberated by means of the sensory fibres of the limb (Brondgeest), and the necessary irritation of which appears to proceed from the skin (Cohnstein). This contraction does not affect all the muscles of the limb, nor has it been shown to exist at all in the ordinary posture of the body. In the first place, as may be proved, it only affects the flexors; and in the second it is but another form of the better known phenomenon that a brainless frog strives, in all positions of body, to retract its legs. It has not yet been proved that, after the legs have been drawn up as in sitting, contraction of the flexors continues in the same manner as during suspension, when retraction, on account of the weight, cannot be maintained, except to a slight extent, for any length of time (Hermann). Hence Brondgeest's phenomenon is to be regarded merely as the special continuance, under abnormal circumstances, of a contraction of reflex origin, which is usually transitory. And therefore the formerly surmised 'muscular tonus' does not exist.

The influence of section of the posterior roots in diminishing the irritability of the anterior (p. 355) may be explained by reference to the above-mentioned phenomenon (Steinmann and Cyon).

The previously-mentioned stimulation of the spinal cord by dyspnœic blood is often not apparent immediately after section of the cord, in consequence of the shock which the section inflicts upon the whole cord. Subsequently, however, dyspnœa may occasion general convulsions, sweating, vascular cramp, fœcal evacuations, contractions of intestine and uterus, &c.; these may also be occasioned by heat, as well as by such poisons as picrotoxin (Marshall Hall, Luchsinger, V. Schroff and others). Rhythmical respiratory movements are said to occur when the excitability of the cord is heightened by strychnia or by heat (P. Rokitansky, V. Schroff, jun.)

CONDUCTION TO THE BRAIN.

The communications of the different 'spinal levels' with the brain must be established by means of *cerebripetal* and *cerebri-fugal* fibres; the former ministering to sensation and liberating reflexes of a higher order, the latter leading to movements due either to the will, to cerebral reflexes, and cerebral automatic actions, or serving as the channels for various inhibitory influences.

The slight knowledge which we possess concerning the paths in the spinal cord along which the characteristic operations of that organ proceed, has been gained partly by direct experiment, partly from observations of pathological conditions, and partly from a study of anatomical arrangement. The experiments referred to consist mainly in observing the effects of partial section of the cord, such as unilateral section, section of individual white or grey columns, section at different levels on the same or on opposite sides, &c. The method mentioned on p. 353 for the discovery of paths of conduction, viz. by stimulation, cannot be applied in the case of the spinal cord, if it be true, as some observers state, that the cord is not irritable to direct mechanical and electrical stimuli (Brown-Sequard, Schiff and Van Deen, S. Meyer). It must be remembered, however, that this statement is opposed by others (Fick and Engelken, Giannuzzi). For, assuming the statement to be true, no stimuli applied to the spinal cord, except those of a chemical nature, which appear to be partially *active*, will produce any results if they do not directly excite the root-fibres of some spinal nerve which happens to be traversing the cord at the point of stimulation.

The fibres of the cord proceeding from the vaso-motor centre must be excepted in the above statement, as every stimulation of spinal cord produces narrowing of all the arteries supplied by fibres given off below the point of stimulation (Ludwig and Thiry, see p. 113). Moreover, all stimulations of the substance of the cord, as was mentioned on p. 113, cause reflex irritation of the vaso-motor centre, and raise the blood-pressure (Ludwig and Dittmar¹). Should the apparent inability of electrical and mechanical stimuli to irritate the cord be really established, notwithstanding the assertions to the contrary of Fick and Giannuzzi, it ought rather to be ascribed to an overpowering irritation of such inhibitory fibres as happen to come in the way of the stimulus than to an absolute inability on the part of any conducting portion of the cord to respond to stimulation. In the latter case, it must be supposed that only axis cylinders of the first kind have the general properties of extra-central nerve-fibres, and that the remaining, specially central, fibres cannot be irritated by the most important nervous stimuli. In order to express that the conducting substance of the cord is only capable of conduction and not of irritation, the terms 'æsthesodic'

¹ Ludwig und Dittmar, 'Ein neuer Beweis für die Reizbarkeit der centripetalen Fasern des Rückenmarks.' Ludwig's *Arbeiten*, 1870.

(capable of conducting sensory impressions) and 'kinesodic' (capable of conducting motor impressions) have been applied to it.

From the effects of partial division of the cord in various ways (Brown-Sequard, Schiff, Setschenow, and others) the following conclusions have been drawn. 1. The conduction of localised sensory impressions, and of motor impressions which are voluntarily restricted to definite sets of muscles, is effected through the white substance. Partial section of the latter severs the connection between the mind and individual regions of the skin and individual groups of muscles. Hence result insensibility to tactile impressions—anaesthesia, and paralysis of voluntary motion. The paths which subserve conduction remain on the same side of the cord as far as the brain, *i.e.* they do not cross the middle line of the cord.

The older statements that the conduction of sensory impulses took place through the posterior white columns, whilst the motor traversed the anterior and lateral columns, have not been confirmed by a recent research (Ludwig and Woroschiloff, see p. 483); according to the results of this research, the only channels of conduction to the brain are the *lateral columns*, and it would appear that in these both sensory and motor paths are mixed. In accordance with this view the lateral columns increase in thickness as they proceed from above downwards (compare fig. 68). The special function of anterior and posterior columns would thus appear to be unknown; they possibly contain the previously-mentioned coordinating fibres which connect the various levels of the cord.

2. The 'pressor' fibres, which proceed from the posterior extremities, course along the lateral columns and cross the cord partially (Ludwig and Miescher¹).

3. Sections through the grey matter do not affect the communications between the deeper parts of the cord and the brain. (For the function of the grey matter in relation to sensory perceptions, see below.)

These facts prove that the grey matter serves essentially for the propagation of reflexes from one level to another, a conclusion which can also be arrived at from a knowledge of the fact that its thickness at any level is proportional to the number of the spinal root fibres which enter at that level (hence the cervical and lumbar enlargements). Inasmuch as the communication between sensory roots and cerebripetal fibres occurs through the grey matter, on account of the resistance opposed by the latter, any sensory stimulation will affect the more cerebripetal fibres the more intense it is; the greater the distance between the spinal nerve roots and the origin of the cerebripetal nerve-fibres from the grey matter, the less will these participate in the state of activity.

¹ Ludwig u. Miescher, 'Zur Frage der sensiblen Leitung im Rückenmark.' Ludwig's *Arbeiten*, 1870.

Every sensory irritation must therefore assume the form of a *sensory circle*, and the area of this must be more extended (that is, the sensation must be the more radiated) the more intense the stimulus. Amongst the ordinary so-called tactile stimuli may be distinguished the intense so-called 'pathic' stimuli, by their greater diffusion and by the correspondingly more diffused and less orderly reflexes which they occasion. Perhaps the greater diffusion (or radiation) is a condition necessary for the perception of pain, as, after section of the grey matter, *analgesia* is observed; *i.e.* that—as occurs sometimes during chloroform narcosis—instruments which are inflicting injuries which normally would be painful are felt, but the sensations are not painful (Schiff); obviously, assuming that a section through the grey matter produces the effect previously mentioned, one must conclude either that the section injures the whole grey matter, or, which is unlikely, that even the grey matter is engaged in conducting in a longitudinal direction to the brain impulses which give rise to pain.

Lastly, voluntary stimulations must, in consequence of the properties of the grey matter, excite a large irradiation circle in it, and therefore throw into activity a certain number of motor nerves. As, further, the occurrence of orderly reflexes already rendered necessary the surmise that co-ordination of different regions are brought about by well-conducting fibres, it is scarcely to be doubted that these are also combinedly thrown into action, so that in the case of orderly voluntary movements the mind is spared a certain amount of work. In respect to inhibitory fibres it must be remembered that those which limit the diffusion of reflexes must also diminish irradiation; but the fact has not actually been determined.

2. Encephalon.

The continuation upwards of the spinal cord, consisting of medulla oblongata, cerebellum, the so-called cerebral ganglia (corpora quadrigemina, thalami optici, corpora striata, &c.), and the cerebral hemispheres, contains a great number of central organs concerning the functions and combinations of which extremely little has been discovered. The cerebral hemispheres contain the organs concerned in the psychical functions, as will be shown hereafter.

One of the chief objects of the physiology of the central nervous system is to investigate the connections between the organ of the mind and the peripheral end-organs, *viz.* sense-organs and muscles. As far as spinal nerves are concerned it has already been shown that they do not proceed directly to the surface of the cerebral hemispheres, but that they first enter the grey substance

of the cord. This substance is then connected with the brain—but still, as will be presently explained, not with the surface of the cerebrum—by means of the longitudinal fibres of the white columns.

Cranial nerves, also, do not communicate directly with the surface of the cerebrum, but first enter certain intermediate central organs, a general view of which is contained in the following statements.

The grey mass covering the cerebral hemispheres gives off the following systems of fibres, which form the white substance of the hemispheres:—1. Fibres uniting together various regions of the surface on one side (so-called ‘associating fibres’). 2. Fibres uniting symmetrical, and perhaps also unsymmetrical, regions of surface of the two hemispheres (so-called ‘commissural fibres’ passing through the corpus callosum and the anterior commissure). 3. Radiating fibres running towards the above-mentioned cerebral ganglia or grey masses lying in the interior of the brain (‘peduncular fibres’). The third system must constitute the bond between the organ of mind and the external world, that is to say, if there is not yet another system (as Broadbent maintains) consisting of fibres which run uninterruptedly from the posterior part of the grey matter through the crura cerebri into the white substance of the cord.

The ganglia at the base of the brain are directly connected with nerves (anterior cranial nerves) and with one another. Finally, the strongest bonds of union pass, by means of the peduncles of the brain, to the cerebellum, and to the grey substance of the medulla oblongata and the spinal cord, and, therefore, to the proximate termination of almost all peripheral nerves.

If we regard as the object of all nervous combinations the projection of the surface of the body, in its motor and sensory aspects, upon the plane of the mental organs, the following schema of this projection may be drawn (Meynert):—The first system of projection, perhaps better described as the inner, unites the cerebral cortex with the large ganglia at the base of the brain (the radial system of fibres); the second system of projection, or the middle system (the peduncles, &c.), unites the basal ganglia with the grey substance of the spinal cord and the analogous portion of the medulla oblongata (viz. the ‘central grey tube,’ so called because the substance composing it lies about the central canal of the cord and its continuation—the *calamus scriptorius*, floor of the fourth ventricle, aqueduct of Sylvius, and third ventricle); the third system of projection, or the external, is constituted by the peripheral nerves. The second is weaker than the others; hence, at the points of union of the three systems there is noticed between the internal and middle a reduction, and between the middle and external again an increase, in the number of fibres. In the middle system a crossing, probably of all the fibres, takes place, i.e. the fibres cross the middle plane to reach the opposite side of the body.

This schema, as might be expected, does not hold in its entirety; deviations from it are observable especially in the case of the anterior cranial nerves, in which there appears to be no organ corresponding to the central grey tube, and,

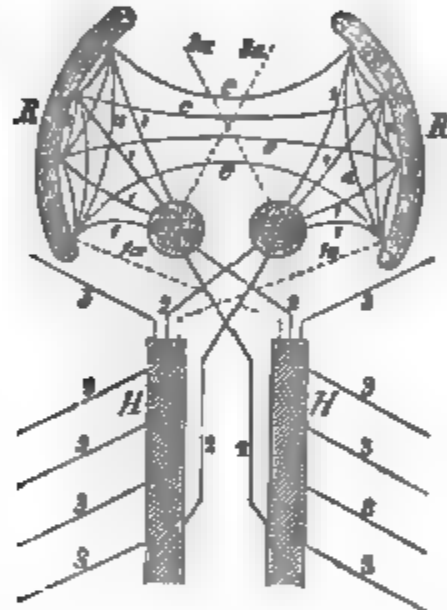
therefore, no middle system of projection.¹ Moreover, the fibres above mentioned, which pass from the grey matter of the cortex direct to the central grey matter, would offer an example of deficiency of the middle system of projection.

The cerebellum forms a centre, laterally situated, which communicates with all the rest, and from which, also, arise nerve-fibres of the external system (portions of the trigeminus and acoustic nerve).

The annexed diagram serves to explain the three systems of projection: *R* is the grey substance of the cerebral cortex, *a* the ganglia at the base of the brain, *H* is the central grey tube, 1 2 3 are the fibres of three systems of projection, *a* are associating and *c* are commissural fibres. The dotted fibres represent the above-mentioned deviations; for example, *3a* represents the optic fibres, and *1a* the combining fibres of Broadbent.

The combinations of the ganglia at the base of the brain one with another and with the grey substance of the spinal cord, and with its cerebral analogue, are the most difficult to determine, and form the weakest portion of the anatomy of the encephalon.

FIG. 69.



Where the spinal cord becomes medulla oblongata the central canal of the former makes its way to the surface posteriorly in the calamus scriptorius, and forms a shallow groove in the floor of the fourth ventricle. The grey substance surrounding the canal at the same time reaches the posterior surface and lies spread out on the floor of the groove, the anterior cornua being external to the posterior. More superiorly the grey substance assumes the form of scattered grey masses, the so-called 'nuclei' of the posterior cranial nerves, which are clearly the analogues of the grey substance of the spinal cord. The main body of the medulla oblongata consists of white columns, the continuations of the white columns of the cord, which run in part to the ganglia at the base of the brain, viz. to the corpora quadrigemina and through the

¹ Many observers believe that, in the nerves of special sense, the peripheral ganglion-cells are the organs which correspond to the central grey tube, considering, for example, the optic fibres as the middle system of projection and the radial fibres of the retina as the external series.

crura cerebri to the thalami optici, corpora striata, and lenticular nucleus, and in part to the cerebellum. From the white posterior columns of the spinal cord those fibres contained in the funiculi graciles and processus cuneati pass through the crura cerebelli to the cerebellum; the rest pass through the external bundles of the pyramids and the crura cerebri into the cerebrum (some, as was mentioned above, passing directly to the cortex of the posterior portion); and a small number of fibres run directly into the trigeminal nerve, which thus gets a spinal root. The anterior and lateral columns run partly through the pyramids and crura cerebri to the corpora striata and lenticular nucleus (and, possibly, in part direct to the cortex of the cerebrum), partly to the corpora quadrigemina and through the tegmentum to the optic thalami, and partly through the corpora restiformia and the crura cerebelli to the cerebellum. The cerebellar hemispheres, which, according to what has just been said, communicate with all the white columns of the cord through their peduncles, are in addition united with the pons, and hence with each other, by means of the crura cerebelli ad pontem; and also to the cortex of the cerebrum, by the crura cerebelli ad corpora quadrigemina, which do not really communicate with the grey substance of the corpora. The medulla oblongata contains, in addition, the hemispherical olivary bodies, about the relations of which little is certainly known.

The following statements embody what has been discovered concerning the origins of the cranial nerves:—

First pair (*Olfactory*). The olfactory tracts lying at the base of the anterior lobe of the brain, and becoming continuous with the olfactory bulbs, are the rudiments of the olfactory lobes of the lower animals—largely developed lobes of the brain analogous in structure to the cerebral hemispheres. Their white fibres communicate with various portions of the cortex of the cerebrum, and, according to some, with the corpora striata also. From the bulbs arise the olfactory nerves proper, which perforate the cribriform plate.

Second pair (*Optic*). The optic tracts arise in part from the corpora geniculata externa and from the thalami optici, and in part from the corpora geniculata interna, and from the anterior corpora quadrigemina. Bending round the crura cerebri, they then form the optic chiasma, in which, according to some, one-half, and according to others, all, the fibres of each tract cross over to the opposite side.

Third pair (*Motores oculi*) and

Fourth pair (*Trochlear* or *pathetic*) arise on each side in the neighbourhood of the aqueduct of Sylvius, from a grey nucleus, common to both, which communicates with the above-mentioned corpora quadrigemina, and also through the crus with the lenticular nucleus. While the *third nerve*, piercing the crus to its under surface, emerges close to the pons, the *fourth* passes upwards, perforates the roof of the aqueduct, crossing at the same time to the opposite side, and bends round the crus, after the fashion of the optic tract, to appear on the surface below.

Fifth pair (*Trigeminal*). The fibres of this nerve have very various origins. *a.* On a level with the point of exit from the pons is the so-called 'trigeminal sensory nucleus,' the ganglionic cells of which are small, which is analogous to the posterior cornu of the grey substance of the cord; from it certain of the fibres originate. *b.* The ascending root is derived from the posterior column of

the cord—and from a portion at least as low down as the middle of the neck—the fibres springing from the grey substance of the posterior cornu and running in the white posterior columns. At the side of the medulla the fibres run for some distance very superficially. This very sensitive part, situated close behind the processus cuneatus, and sometimes but slightly developed, is the tuberculum Rolandi. *c.* Descending roots, viz. (1) from the large-celled 'trigeminal motor nucleus,' in the neighbourhood of the corpora quadrigemina, concerning the further connections of which with the ganglia of the brain nothing is known; (2) from a collection of large vesicular cells (similar to the cells of the spinal ganglia) at the side of the aqueduct of Sylvius; (3) from the locus cæruleus which lies beneath the *substantia ferruginea* in the upper part of the floor of the fourth ventricle, the fibres being crossed. *d.* Fibres from the cerebellum, running in the crura cerebelli ad corpora quadrigemina.

Sixth pair (*Abducens*). The fibres of this nerve arise from a large-celled nucleus at the bottom of the groove in the floor of the fourth ventricle, at its anterior part. The further connections of this nucleus, which supplies fibres to the facial, are unknown.

Seventh pair (*Facial*). This nerve is derived from a nucleus similar to the one last mentioned, though situated somewhat lower, but receives a number of fibres also from the nucleus of the sixth nerve. Another, descending, set of fibres come from the lenticular nucleus of the opposite side of the body. The connections of the nucleus of this nerve are unknown.

Eighth pair (*Auditory*). This nerve receives fibres chiefly from three interdependent nuclei, which lie on a level with the broadest (middle) portion of the floor of the fourth ventricle between and in front of the corpora restiformia. Fibres both from these nuclei and from the trunk of the auditory nerve may be traced into the crura cerebelli and into the cerebellum, but the other relations of the fibres of the auditory nerve are not as yet known. A portion of the fibres cross between the nucleus of origin and their place of exit.

Ninth pair (*Glossopharyngeal*) and

Tenth pair (*Par vagum, pneumogastric* or *vagus*) arise from the nuclei, which are, in part, common to both, situated in the lower half of the floor of the fourth ventricle, and in the substance of the medulla oblongata near the olivary bodies. These nuclei supply fibres to the spinal accessory also. Their connections are not known.

Eleventh pair (*Spinal accessory*). In addition to the fibres from the nuclei just mentioned, this nerve is supplied from an elongated nucleus lying along the external surface of the anterior cornu and reaching as far down as the fifth cervical vertebra. The fibres leave this nucleus in a great number of roots, which lie in a special line down the lateral column of the spinal cord between the anterior and posterior roots of the cervical spinal nerves. This line is somewhat spiral, being more posterior below.

Twelfth pair (*Hypoglossal*). The fibres of this nerve arise, for the most part, from two large-celled nuclei, situated deeply in the substance of the medulla oblongata, on a level with the lowest portion of the floor of the fourth ventricle. Some of the fibres appear to arise higher up in the brain without touching the nuclei. Certain observers have maintained the existence also of connections with the olivary bodies.

The statements of anatomists are too incomplete and insecure for the establishment of any theory concerning the functions of the various parts of the brain. Theories have, however, been set up notwithstanding the deficiency of facts at our disposal. Such a one, for example, is that of Meynert, according to which that division of the crura cerebri which is known as the *basis* or pedunculus (in the limited sense) which is connected with the lenticular nucleus and corpora striata, and which is developed in the various

members of the animal series proportionately to the cerebral hemispheres, is concerned in the conscious reception of sensations and in the production of movements; while that portion of the *crus* which is known as the *tegmentum*, and which communicates with the optic thalami and the corpora quadrigemina is concerned in the reflection of impressions from the optic nerves into the motor apparatus.

Physiological experiments conducted in these regions are most indefinite. The usual plan of investigation, viz. that of applying stimuli to the brain-substance, leads either to negative results, or, if electrical stimulation is used, to results which, owing to the unavoidable dispersal of the currents in numerous directions, are not sufficiently localised to form the basis for trustworthy conclusions. In the place of exact observations after section and stimulation of different regions, we have here the far less refined method of observation after lesions—lesions induced in the most delicate and complicated organ of the body by means so absurdly rough that, as Ludwig has forcibly put it, they may be compared to injuries to a watch by means of a pistol shot. The results obtained in this way are attributable to the most diverse causes; for, apart from the fact that it is impossible to localise the lesion itself, the results may be due to irritation of centres, paralysis of centres, stimulation of conducting apparatus, or paralysis of conducting apparatus, without our being able to say to which. Hence the interpretation of even those phenomena which are constant in their occurrence is always uncertain.

The third and best method of investigation which is possible is the observation of cases of disease in which the exact nature of the lesions is accurately ascertained after death.

The facts which may be considered in some degree established are the following:—

A. Medulla Oblongata.

In the medulla oblongata essentially the same arrangement of parts is noticed as in the spinal cord. The grey substance, the connections of which with that of the spinal cord, and with the cranial nerves from the sixth (abducens) downwards, have already been described, is, without doubt, the seat of manifold reflex processes in which those nerves are implicated, and of a number of motor impulses, some of which (if not all, as some think) are to be regarded as reflex in their nature, others as automatic. The functions in which the medulla is concerned are of such importance to the whole organism that injuries of this portion of the encephalon are more dangerous to life than those of any other region of brain or spinal cord.

1. *The Centre for the Involuntary Movements of Respiration,*

and for the Convulsions of Dyspnœa.—Lesion of a limited region of the floor of the fourth ventricle at the apex of the calamus scriptorius causes sudden cessation of respiration, and instant death to warm-blooded animals. This region is called *le nœud vital*, or *point vital* (Flourens¹). It extends on both sides of the middle line; and, if the lesion affect one side only, the respiratory symptoms affect the corresponding side of the body alone.

According to more recent statements (Gierke²), the structure, injury to which abolishes respiration, does not consist of a mass of ganglia, but of two bundles of fine nerve-fibres, which spring in part from the vagus-fibres entering them, and in part from the nuclei of the vagus and trigeminus, and which run towards the spinal cord, whence the proper respiratory nerves arise. While extirpation of the individual nuclei is not alone sufficient to cause respiration to cease, destruction of this, partly intercentral and partly, even, merely centripetal, combination between vagus, trigeminus, and spinal origin of respiratory motor nerves, produces paralysis of respiration. The view that this nervous union constitutes essentially the 'respiratory centre' seems, however, inadmissible, for the *rhythmical* character of the excitation can scarcely originate otherwise than in some ganglionic apparatus. It is quite possible that this ganglionic apparatus is situated in the spinal cord itself, if, as stated, animals poisoned by strychnia still breathe after section of the cord in the cervical region. (P. Rokitsansky.)

It is not yet established whether this centre liberates the rhythmical movements of respiration automatically, or whether its activity is dependent upon the excitation of centripetal nerves, and is, therefore, reflex in its nature (compare p. 202). The respiratory centre is the only centre concerning which the conditions of the automatism (or the reflex powers) are at all fully understood. Its activity requires:—1. The presence of oxygenated blood, without which irritability disappears. 2. A certain relationship among the gases of the blood, which relationship acts as a stimulus; the smaller the amount of oxygen, and the larger the amount of carbonic acid, present in the blood, the more intense becomes the activity of the centre, and the greater the number of muscles which are brought into play (Dyspnœa); if the amount of carbonic acid present sinks below a certain point, the activity ceases altogether (Apnœa). More exactly speaking, the respiratory centre consists of two centres, the rhythmical activities of which, although apparently independent as to strength, alternate as to the time of their phases, viz. one being connected with the inspiratory and the other with the expiratory muscles. Each supplies a definite group of muscles, the members of which, however, are not all equally implicated in movement, more or fewer being rendered active according to the strength of the exciting cause, which varies in proportion as reflex processes are extended in the spinal cord. Moreover, these centres possess accelerating and inhibitory nerves, in the

¹ Flourens, 'Recherches sur le système nerveux.' *Comptes Rendus*, 1847, 1851, 1858, 1859, 1862.

² Gierke, 'Die Theile der Medulla oblongata, deren Verletzung die Athembewegungen hemmt, und das Athemcentrum.' *Pflüger's Archiv*, vol. vii. p. 583.

sense in which the terms were explained on p. 474. Stimulation of those nerves, whose course has already been given (p. 201), does not seem in general to increase or diminish the activity of the centre, but merely to modify the distribution of the activity in time. The fibres which produce on irritation slowing of the movements of inspiration cause at the same time quickening of those of expiration, and *vice versâ*.

The rhythm of respiration may be best illustrated by the example already given of gas conducted through a tube under water, only, in this case, the gas must be supposed to be led through a *forked* tube, the limbs of which dip into different fluids. One of these fluids—that representing the normal resistance to inspiration—must be supposed to be considerably less cohesive than the other, representing that of expiration. Irritation of the vagus corresponds to diminution, and irritation of the superior laryngeal nerve to increase, in the cohesiveness of the first fluid. Dyspnoea corresponds to increase of the pressure under which the gas is forced through the tube. The bubbles which stream up through the first fluid represent the nervous impulses transmitted to the inspiratory apparatus; those which ascend through the second correspond to the impulses transmitted to the expiratory mechanism. The illustration shows at the same time that, for simple reasons, in the case when bubbles rise in both tubes (*i.e.* when inspiration and expiration are both *active*), they ascend alternately, first in the one and then in the other.

The increase in the frequency of respiration under increased temperature may be produced by raising the temperature of the brain alone, which may be accomplished by placing the carotids in heated tubes (Fick and Goldstein). It is therefore considered to be dependent upon changes occurring in the respiratory centre. At high temperatures artificial respiration does not produce apnoea (Ackermann).

If excitation of the respiratory centre reaches an abnormal strength, other muscles besides the normal and accessory muscles of respiration are brought into play, *viz.* in the first place, the muscles of the jaws, as in gasping, and finally almost all the muscles of the body, as in the general epileptiform convulsions attendant upon suffocation. This is clearly a mere case of extension of the condition of excitation throughout the grey substance of the medulla, and perhaps also of the cord; and, as a fact, other nervous centres in the medulla are implicated, as the centre for the dilatation of the pupils, the vaso-motor centre, and the cardio-inhibitory centre. Some observers explain the phenomenon by assuming the existence of a special 'convulsion-centre' in the medulla.

These convulsions occur not only when the interchange of the gases of the blood is prevented, but also when the blood, or the substance of the brain, is deprived of oxygen or is saturated with carbonic acid, as, for example, when the blood in the blood vessels of the brain stagnates in consequence of ligature of all the afferent arteries, or when excessive bleeding has occurred. These observations (Kussmaul and Tenner) have led to the designation of 'con-

vulsions of anæmia,' a term which is now no longer admissible since the true nature of the process is understood (Rosenthal), and since it has been found possible to produce the same convulsions by causing venous blood to stagnate in the vessels (Hermann and Escher).

According to researches, in which the medulla was directly stimulated, the above-mentioned convulsions occur on irritation of a region which (in rabbits) is bounded above by the corpora quadrigemina, below by the *alæ cineræ*, externally by the locus *cæruleus*, and acoustic tubercle, and internally by the *eminentiæ teretes*. This region, which is stimulated to activity by the presence of asphyxial blood, is not supposed to be the real 'convulsion-centre,' but merely a point from which radiate impulses to movement, which are derived from a reflex convulsion-centre situated in the pons (Nothnagel). The action of certain poisons which induce clonic spasms—especially picrotoxin, nicotin, barium salts, &c.—has lately been referred to a stimulation of this centre (Röber, Heubel, Böhm).

2. *The Centre for the Regulation of the Heart's Action.*—The centre whence the inhibitory vagus-fibres for the heart receive their stimulation (which, as was explained on p. 110, is possibly rhythmical in its nature) lies somewhere in the medulla oblongata, but its precise situation is not yet known. In warm-blooded animals the centre is constantly active, not, however, as has hitherto been assumed, automatically, but as a consequence of reflex stimulations; for section of certain centripetal nerves releases the 'tonus' of the vagus (p. 110), and, according to Goltz and Bernstein, irritation of them increases its inhibiting powers. It has not yet been determined whether the accelerating nerves of the heart also, which will be described when the sympathetic system is treated of, have their centre in the medulla oblongata.

3. *The Vaso-Motor Centre.*—The general vaso-motor centre lies certainly higher than the commencement of the cord, for section of the cord in the cervical region paralyses all the arteries of the body (Ludwig and Thiry, p. 113). It extends in rabbits from about 3^{mm} above the *calamus scriptorius* to the upper portion of the floor of the fourth ventricle, but its upper boundary cannot exactly be determined; and is situated bilaterally, at some distance from the middle line, in that portion of the medulla which contains the continuation of the lateral spinal columns, in which, as has been already stated, the vaso-motor and pressor fibres run. It contains some large multipolar ganglion-cells (Owsjannikow, Dittmar). It is constantly in action, and its activity is either automatic or, perhaps, merely reflex. The facts in connection with this activity and the influence exerted upon it by the gases of the blood and by the regulating nerves have been already stated (pp. 114 and 115). The fibres proceeding from the centre pass into the cord, and, after having probably been first interrupted by the grey substance in the manner indicated in the section on arterial tonus, leave it again, set by set, in order to be distributed to

the arteries, for the most part along with fibres from the sympathetic system. Hence, section of the spinal cord causes dilatation of all the arteries in the regions below the point of section, while its irritation produces the opposite condition of contraction (Ludwig and Thiry), the former diminishing and the latter increasing the blood-pressure and temperature of the organism, and acting on the heart in a corresponding manner.

Irritation of the *crura cerebri* causes contraction of all arteries (Budge). This circumstance does not disprove the former statement that the proper vasomotor centre lies in the medulla; it merely shows that the cerebrum can exert some influence upon that centre—blushing and growing pale, due to psychical causes (Budge); the reader should refer also to the effects of removal of the cerebrum upon the action of sensory nerves (p. 115).

4. *The Centre for the Dilatation of the Pupils, and for the Movements of the other Smooth Muscles of the Eye.*—The exact position of the centre which gives off fibres to the oculo-spinal region of the spinal cord is not known. The centre itself, wherever it be, is constantly active, and, possibly, owing to reflex stimulation. It is under similar influences to the respiratory and vasomotor centres, dyspnoea, for example, being accompanied by dilatation of the pupils whilst the optic vessels become pale.

5. *The Centre for the Movements of Deglutition.*—The proof that this centre is situated in the medulla oblongata chiefly rests upon the occurrence of convulsive movements of swallowing when that portion of the nervous system is under stimulation, and upon the anatomical fact that the nerves concerned in the act are derived from the medulla. The exact situation of the centre is not yet determined. The centre is only called into activity by reflex stimulations, and must therefore be put into the same category with the numerous apparatuses in the spinal cord for orderly reflex actions.

6. *The Centre for the Movements of Mastication.*—The proofs of the existence of this centre in the medulla are similar to those referred to in the case of the last-mentioned centre, viz. the occurrence of trismus or cramps of the masticatory muscles under similar circumstances to those mentioned above. The centre resembles the spinal apparatuses for orderly reflex actions which are also employed in regular voluntary movements.

7. *The Diabetic Centre.*—Lesions of a portion of the floor of the fourth ventricle near the middle line, and extending from a little above the calamus scriptorius to the broadest part of the groove, cause transitory diabetes (p. 220), or sometimes merely increased secretion of urine—diabetes insipidus (Bernard). The supposition which was formerly held that this was due to irritation (or, according to others, to paralysis) of a centre for the nerves regulating the formation of sugar in the liver, and which was connected with the vagus, is rendered doubtful in consequence of the

altered views of physiologists concerning the processes occurring in the liver (p. 218). Many suppose, as is elsewhere recorded, that it is due to injuries inflicted upon the vaso-motor centre in this region of such a nature as to cause dilatation of the vessels of the liver, kidneys, &c.

The other functions of the medulla oblongata are not well understood, with the exception of those concerned in the reflex actions already mentioned, in which the lower cranial nerves play a part, as, for example, in the reflex operations in the production of saliva (p. 131). The use of the olivary bodies is entirely enigmatical. The crossing of the fibrous tracts in the medulla, as well as certain kinds of involuntary movements which follow injuries to it, will be discussed below.

Many of the above-named centres in the medulla oblongata are functionally associated together, as may be gathered from the coincidence of their rhythmical activity. Thus at the commencement of each expiration a slowing of the pulse commences, which depends upon a vagus-excitation which coincides with the end of inspiration, and the effect of which is somewhat delayed by the latent period (Donders, Pflüger); further a periodicity is noticed in the vascular spasm of dyspnœa which is synchronous with respiration. Finally dyspnœic stimulation acts on many of the centres of the medulla oblongata, producing by varied actions dyspnœa, muscular spasms, vascular spasm, dilatation of pupils, slowing of the pulse, secretion of saliva, &c.

This survey of the functions of the medulla oblongata shows that in addition to 'reflexes in one plane,' of which it is the seat (analogous to those which occur in the spinal cord), numerous additional acts of a higher order here take place, which exert an influence upon the spinal cord. In discussing the spinal cord it has already been mentioned that reflexes between different spinal levels chiefly occur through the intermediation of the spinal cord. Recent researches have shown that even the vaso-motor centre represents nothing but an association of spinal centres. The same holds true in the case of the centre which presides over spasms, as even the separated spinal cord is capable of dyspnœic and toxic spasms; the same is actually held in reference to the respiratory centre.

The function of the olivary bodies is altogether doubtful. Concerning the decussation of fibres in the medulla oblongata, as well as for a discussion of the 'compulsory movements' which occur when these are injured, see below.

B. Ganglia at the Base of the Brain, and White Substance of the Brain.

The region between the medulla oblongata and the surface of the cerebral hemispheres contains a number of extensive grey

masses—the ganglia already enumerated—and a highly complicated system of white fibres, the general distribution of which has also been given.

In the lower vertebrates, *e.g.* in frogs, it may be shown that, after the power of conscious action has been abolished by removal of the cerebral hemispheres, the possibility of a number of complicated movements still remains, but that these cease when the other parts of the encephalon situated above the medulla are removed. The animals experimented upon are, more particularly, enabled to maintain their equilibrium under varying conditions, and (for example) to prevent themselves, by properly adapted movements, from slipping down a plane the inclination of which to the horizontal is gradually increased (Goltz). Moreover, in these regions, in frogs chiefly in the optic lobes which correspond to the corpora quadrigemina and thalami optici, are situated the arrangements whereby the reflex powers of the spinal cord are inhibited (Setschenow). The ganglia at the base of the brain are not only in communication with the grey substance of the cord and medulla, and, through these, with almost all the peripheral organs of the body, but are also connected with the nerves of the higher senses, whereby they are concerned in much more manifold and complicated centripetal excitations than are the simpler reflex apparatuses of the cord; hence it would seem that they are the seat of reflex operations and co-ordinations of correspondingly greater complexity; for the complexity of the efferent or centrifugal impulses to activity must increase with the number of afferent or centripetal stimulations. The importance of this region is apparently still further increased by the fact that, besides possessing the means of bringing about excitations in the subordinate groups of centra which it contains, it has the power of inhibiting reflex action. The above-mentioned power of adjusting equilibrium is probably but one slight indication of the functional powers possessed by these organs. The participation of the higher nerves of sense in those powers will be understood when it is remembered that, in the first place, the objects in the field of vision, as well as the muscular sense of the muscles of the eye, influence powerfully our movements; and that, in the second, the auditory nerve is most probably connected with peripheral apparatuses which serve to explain the position of the head; and to these circumstances may be added the centripetal impressions from the whole skin, and from the muscles, the influence of which upon the posture of the body has already been stated.

With the above properties of the portions of the brain now being considered must probably be connected the circumstance that unilateral lesions affecting them give rise to extremely abnormal movements, '*uncontrollable movements.*' The chief forms of these abnormal movements are: (1) movement forwards at the

periphery of a circle—like that of a horse galloping round a ring; (2) rotation about the longitudinal axis of the body—rolling or waltzing movements; (3) movement of the anterior portion of the body about the fixed posterior portion. They follow injuries to the corpora striata, optic thalami, crura cerebri, pons Varolii, and certain portions of the medulla oblongata and cerebellum. More exact statements as to the form and direction of the movements cannot with certainty be given. Their direction changes, in consequence of the crossing of fibres, according as the plane of the section is more anterior or posterior. The older explanation which assumed the existence of centres for the production of movement in a certain direction which were stimulated by these injuries, is inadmissible, because the movements frequently occur merely as abnormal expressions of an intentional movement, such as of flight. Moreover, lesion of white fibres, as of the crura, is sufficient to produce them, and they have been sometimes observed to follow injuries to the cortical portion of the cerebrum. Mere paralysis of individual groups of muscles—for instance, in the case of the first class of abnormal movements previously referred to, of the muscles of the side of the body turned towards the imaginary centre of the circle of movement—is also insufficient to explain the phenomena, for this paralysis frequently does not exist.

The resemblance between uncontrollable movements and those occasioned by rapid passive rotation points to the former being due to the action of sensations of vertigo, *i.e.* they depend upon delusions on the part of the animal as to its moving in a particular direction, or as to the movements of the surroundings; these delusions which arise through lesions in the organs which are concerned in the perception of movements being answered by reactive movements. Even in the absence of consciousness, these reactions occur purely as reflexes. This explanation would postulate the existence of definite organs situated in the parts of the brain referred to, concerned in loco-motor sensations, and would ascribe the reactive movements to these organs—a conclusion which agrees with inferences from other previously-mentioned facts.

As the determination of the position of the body in space occurs especially through the association of the objects seen with the appreciation of the position of the eyes and head, there are associated with the phenomena of vertigo abnormal positions of the head and eyes; in cases of 'uncontrollable movements,' due to injuries of the brain, the position of the head is generally abnormal. On passive rotation of a man or of animals the eye-balls always lag behind, and turn in a spasmodic manner ('nystagmus'); this movement, which continues afterwards for some time, leads, when the surrounding objects are still, to the impression of a rotation in the opposite direction (which, however, even occurs when the eyes

are closed). A peculiar vertiginous phenomenon occurs on passing a galvanic current through the head (Purkinje¹), being most violent when the electrodes are placed on the mastoid processes (Hitzig²). The objects surrounding the patient appear, when the current passes from left to right, to turn in the direction of the hands of a clock; but, on breaking the current, in the opposite direction; thence occurs a corresponding 'nystagmus' and a reactive movement of the body, which, when the current is intense, may become an uncontrollable ('waltzing') movement; the apparent movement of surrounding objects appears to be the consequence of the nystagmus. Galvanic vertigo probably depends upon the action of the current upon the mid-brain. The recently-investigated explanation that the vertigo is due to an action upon the assumed organs in the labyrinth, is disproved by the fact that galvanic uncontrollable movements may occur even after section of both auditory nerves (Tomaszewicz).

Our knowledge of the special functions of individual ganglia is most incomplete. The corpora quadrigemina, which communicate on the one side with the optic nerve and on the other with the nucleus of the motor oculi, may be shown, both anatomically and experimentally, to form an important reflex centre between the retina and the internal and external muscles of the eye. After destruction of these organs, reflex contraction of the pupils ceases; irritation of them produces contraction of the pupil of the opposite side, or, according to others, of both sides (Flourens, Longet, Budge). According to more recent statements (Knoll), the above results are said to occur only when the optic tract is implicated, in which case the corpora quadrigemina would not be a centre for the reflex contraction of the iris. On the contrary, stimulation of the anterior corpus quadrigeminum is asserted to cause dilatation of the pupil of the same side, as long as the cervical sympathetic cord remains intact, and therefore to stimulate the centrum ciliospinale. Stimulation of the anterior corpus quadrigeminum also causes rotation of both eyeballs towards the opposite side (Adamük).

The thalami optici, which also communicate with the optic nerve, do not admit of experimental investigation without the most extensive injury of other parts of the brain. As lesions of the optic thalami produce the peculiar movements above referred to, it is supposed to be through them that the eye influences coordinated movements. Pigeons whose cerebra have been extirpated without injury to the thalami optici follow by movement of the head the direction of a light which is carried round them in a circle (Longet). The intimate connection of the optic thalami with the cortex of the cerebrum indicate, in addition, functions concerned in the conscious perception of visual impressions.

¹ Purkinje, *Russ's Magazine*, 1827.

² Hitzig, *Untersuchungen über das Gehirn*.

Scarcely any facts, save those of an anatomical nature, are known respecting the corpora striata and lenticular nucleus. These organs, which, like the fibres of the crura proceeding to them, have a proportionate development to the cerebrum in the various classes of animals, probably take a part in the production of conscious sensations and movements, which is, however, quite unknown. Lesions of the lenticular nucleus invariably cause hemiplegia. A species of spasmodic attempt at flight has been recently noticed to follow injuries to the corpora striata (Nothnagel).

Nothing whatever has been discovered with regard to the physiological position and function of the numerous grey tracts of the pons Varolii.¹

In the mass of white substance extending between the ganglia at the base of the brain and the central grey substance an apparently complete crossing of the fibres from one side to the other takes place. The physiological proof of this lies in the circumstance that pathological changes and injuries situated in one of the cerebral hemispheres are followed by anæsthesia, or paralysis of voluntary motion only in portions of the *opposite* side of the body. Not until the lesion has affected—by pressure, &c.—the cranial nerves situated at the base of the brain, do symptoms manifest themselves in portions of the head situated on the *same* side as that of the seat of injury. As to the exact situation where the crossing takes place, the discoveries of anatomists and physiologists do not quite agree. For example, while dissection shows an intercrossing of fibres of the white columns in the anterior white commissure of the cord, unilateral sections of those columns are only followed by paralysis of the same side (Volkmann, von Bezold). The crossed commissural fibres are, therefore, possibly merely co-ordinative in function, like those marked 4 in fig. 68. Fibres cross over from one side to the other in various situations of the spinal cord: firstly, between the pyramids, where, to judge from the connection with the columns of the spinal cord, both motor and sensory fibres are concerned in the crossing, the former, however, passing over at a lower point; secondly, in the white raphe or white lamina occupying the mesial plane of the medulla, where occurs, especially, the crossing of the connecting columns between the grey nuclei of the cranial nerves and the cerebellum, as well as of the fibres running from the nuclei to the peduncles of the brain; and, thirdly, in the pons Varolii, about the crossing of the fibres of which but little is known. The crossing is completed in the peduncles of the brain.

The olfactory, optic, and trochlear nerves form very remarkable exceptions to the general rule of the intercrossing of nerves.

¹ It may be here mentioned that nothing is known of the physiological significance of the pituitary body and pineal gland.

The olfactory fibres are entirely unilateral. The optic fibres cross *outside* the brain in the *chiasma*. According to some the crossing is only partial, extending to half the number of fibres; but it has recently been stated, in support of the view of the entire crossing, that section of the optic nerve causes dilatation of the pupil of the same side, while section of the optic tract causes dilatation of that of the opposite side (Knoll). The same author also states that section of the optic nerve completely releases the tonus of the sphincter iridis, so that section of the motor oculi nerve no longer causes dilatation of the pupil; and that, therefore, the tonus of the sphincter muscle must be regarded as of reflex origin. The trochlear nerve crosses the middle line *after* its exit from its nucleus, as well as while within the substance of the brain; if the crossing of the fibres within the brain is complete, the twofold crossing will of course constitute the nerve practically unilateral. The physiological and pathological facts, which might serve to throw light upon this point, are still wanting.

C. Cerebellum.

The cerebellum was formerly, but on insufficient grounds, thought to be the seat of certain psychical functions, as of the sexual instinct (Gall) and certain other voluntary acts. Pathological facts and the results of extirpation seem to indicate that it rather resembles the above-described organs in containing a great co-ordinating centre for orderly movements (Flourens, Longet, R. Wagner). Awkwardness in performing movements, frequent falling, and, in birds, the loss of the power of flight, are consequences of its removal, or of disease in its tissues. The connection of the cerebellum with all the columns of the cord, with the ganglia at the base of the brain, and with the cortex of the cerebrum, but especially its intimate relations with the auditory nerve, also renders the above function to a certain extent plausible. It is possible that the auditory nerve, the influence of which in judging of the position of the head has already been repeatedly mentioned, plays a similar part to that of the optic nerve in the co-ordinating apparatus of the middle brain. Deafness does not follow on removal of the cerebellum. In disease of the cerebellum affecting one side only, the disturbances of movement appear chiefly to concern the opposite side of the body. Irritation of the cerebellum causes, according to most writers, neither movements nor, as far as can be judged, sensations of pain; recently, however, it has been stated that movements of various kinds follow stimulation (Nothnagel). [By electrical stimulation of the cerebellum in monkeys, rabbits, and cats, Ferrier¹ obtained definite movements

¹ Ferrier, *The Functions of the Brain*. London, Smith, Elder and Co., 1876. See p. 87 et seq.

of the eyes, with which were in some cases associated movements of the head and trunk. He observed further that contraction of the pupil occurred on the eye corresponding to the side of the cerebellum stimulated.]

D. Cortex of the Cerebrum.

The cortex of the cerebrum must be regarded as the chief, if not the exclusive, seat of psychical activity. The essential proofs of this are the following: 1. In the animal series the cerebrum is found to be more fully developed in comparison with the mass of the body, and with the encephalon as a whole, in those classes in which the individuals approach, in mental powers, the condition of man. The degree of development is judged of by the weight of the cerebrum and by the number of gyri or 'convolutions,' for an increase in the latter increases the extent of the superficies, and hence the amount of grey substance. 2. In cases where the cerebrum is abnormally small from birth (*microcephalus*, *cretinismus*), or where it is diseased (*hydrocephalus*, &c.), there is noticed a corresponding diminution in the higher mental powers, or idiocy. 3. Injuries, compression, and diseases of the cerebrum are almost always accompanied by mental disturbance—peculiarity of demeanour, insensibility, somnolence, or excitement. 4. Removal of the cerebral hemispheres (which is best accomplished in birds) induces a condition resembling that of sleep, in which all voluntary movement ceases. Nevertheless, movements of a reflex nature occur in response to the stimulation of sense-organs; but they are so regular in the order of their occurrence that they may be predicted. When the cerebrum is removed in slices, a gradual loss of all the powers of the mind is said to take place (Flourens).

It has been also maintained that the various degrees of mental ability in man are dependent upon the size, development, and weight of the cerebrum; the results obtained *by weighing* are far from supporting this supposition. The height, breadth, and prominence of the forehead are regulated by the development of the cerebrum; and a measure of the prominence is obtained in the 'facial angle,' or angle formed by the intersection of two lines, one of which touches the most prominent point of the forehead and the symphysis of the two halves of the upper jaw, and the other passes through the base of the skull. The more acute is this angle, the more nearly the face resembles the type of that of the lower animals. The relative development of the cerebral hemispheres is best estimated in animals by comparing them with the *corpora quadrigemina*, the size of which has evidently no connection whatever with the degree of psychical development. The cerebra of *Monotremata* and *Marsupialia* amongst mammals are distinguished by the circumstance that they want a *corpus callosum*. Of the sulci the fissure of Sylvius, which separates inferiorly and laterally the temporal and frontal lobes, is the most constantly found; in many mammals (in mice, moles, shrews, and bats) it is the only one present, while in others (in hares, guinea-pigs, beavers, &c.) a few longitudinal furrows and convolutions are added on to the convex surface. In dogs the fissure of Sylvius is surrounded by three concentric furrows, whereby four 'primary convolutions' are formed; at the same time a transverse sulcus occurs in the

anterior part of the brain, which runs from the upper part of the longitudinal fissure, and is called the 'fissure of Rolando,' or 'sulcus cruciatus,' and which is surrounded by the fourth primary sulcus. In many mammalian brains, possessed of a great number of convolutions, the primary convolutions are more difficult to make out.

It is impossible here to enter upon the description and nomenclature of the complicated convolutions of the human brain.

The nature of psychical operations requires discussion here only in one of its aspects. States of consciousness, or *mental operations*, which are connected in some unknown way with the material processes of the encephalic organs, entirely elude definition, as has already been said in the Introduction. But it is another question, and one which may engage our attention here, whether the material processes of those organs form connecting chains between centripetal and centrifugal excitations—a species of complicated reflex actions—which are independent of the states of consciousness, or mental operations, and to which the latter are attached merely as passive concomitants; or whether the latter can actively interfere in the material processes, and so of themselves produce excitation in an organ. The first view seems not to be in agreement with the existence of a *free will*; for it has not yet been determined whether *the same series of centripetal impressions would not constantly induce in the same organism exactly the same effects, i.e. would call forth the same apparently voluntary movements*. The second view presents the difficulty of requiring the assumption that a scientifically undefinable process acts upon material particles which obey physical laws.

An essential difference between psychical processes and orderly reflex acts lies in the fact that in the latter it is only centripetal stimulations *acting at the time* which are of effect in inducing them, while, in the former, centripetal excitations *which have long gone by* may also operate. It is therefore necessary, from the materialistic point of view, to assume the existence of apparatuses in the mental organs in which centripetal excitations leave behind them a *lasting* change whose psychical expression is '*memory*.' As to the nature of these changes, there exists no ground whatever for speculation.

On the other hand, we are only entitled to assume the existence of psychical functions in cases where the motor reaction following sensory stimulation may be recognised as the associated effect of a past excitation. The other means of deciding the point, viz. the existence or non-existence of states of consciousness, is impracticable, as, strictly speaking, it is impossible to know whether such states occur or not in foreign organisms. Hence we are not justified in ascribing psychical functions to the spinal cord on account of the purposive reactions of headless animals, or of animals asleep, which were previously referred to; for these actions are evidently merely the result of a momentary stimulus, as is

shown by the regularity of their occurrence, and are to be regarded, therefore, as pure reflex actions.

From what has been already stated, a general *schema* of the central nervous system may be constructed: A primary centre ('the central grey matter of the cord'), having apparently no direct connection with the nerves of the higher senses, provides for the simplest reflex acts, in which, essentially, the organs in the vicinity of the body take a part when excited: this, the simplest kind of reflex actions, we have described as 'reflex acts in one plane.' A second centre of a higher nature ('ganglia at the base of a brain, cerebellum (?)'), which is connected with all the regions dependent upon the first centre, and in addition with the higher nerves of sense, and which possesses also inhibitory fibres controlling the first-named centre, provides for more complex actions and reflex actions, in which distant parts of the body are concerned, *e.g.* reactions of the extremities following visual impressions, locomotions which are directed by the eye, &c. A third centre of the highest kind ('cortex of the brain'), which is in connection with the others, has the property, on the application of certain centripetal impressions during the waking state (?), of becoming so changed for considerable periods, or for ever, that unequal complicated actions may result; for, in addition to the manifold combinations of momentary centripetal impressions, numerous impressions of the past also have a distinct action in centrifugal excitation. The number of the possible combinations is, therefore, so immensely great that there is ample scope for theory to explain all actions as the results of centripetal influences. Excitation of this highest centre is accompanied by states of consciousness, and here is the limit of physiological observation.

It is not possible to give more detailed statements as to the arrangements in the centres of the cortex of the cerebrum. The entirely gratuitous phrenological division of the *mental functions* according to 'impulses,' and the equally baseless localisation of them in regions of the cerebral cortex, have long been recognised as meaningless and false. It is also impossible to assign any individual spot in the cerebrum as the seat of consciousness, since cases are known, in connection with almost every part, in which, when that part was destroyed or was wanting, consciousness still remained. Local defects in the cerebrum merely separate certain regions of the body situated on the opposite side from connection with the mind, while consciousness may still remain after destruction of one hemisphere. Unfortunately, we possess no trustworthy experience as to whether, after such destruction, any portion of the images impressed on the memory have been effaced, or as to the connection which exists eventually between the place of injury and the loss of memory.

Unilateral injuries, induced by rupture of the white substance

of either hemisphere, indicate that the mind communicates with the various regions of the body by means of definite fibres. The question now arises, Do these groups of fibres spring from definite regions of the cerebral cortex, or from diverse regions, or even from all portions? The first of these possibilities seems to be supported by the circumstances that pathological changes affecting a certain anterior portion of the brain, namely, the *Island of Reil* (which is situated at the bottom of the Sylvian fissure, and which is discovered projecting downwards between the two branches of the fissure), as well as lesions of the grey lamina of the *claustrum*, which is situated between the *Island* and the lenticular nucleus, induce a condition called 'Aphasia,' in which the patient is unable to speak words while retaining the power of writing them.

Most cases of the above-mentioned 'Aphasia' depend upon lesions of the *left* hemisphere, and are accompanied by paralysis of the *right* half of the trunk (*right-sided hemiplegia*). It has therefore been concluded, not without opposition, that the so-called 'centre of speech' is unsymmetrical—unilateral. Cases are, however, known of Aphasia following lesion on the right side (Bouillaud), and the greater frequency of the former kind is referred to circulatory agencies.

The knowledge derived from experiment concerning the individual sensory and motor functions of the cortex is in the highest degree indefinite. Mechanical lesions occasion, according to most authors, neither pain nor movements. The movements which have recently been induced (Fritsch and Hitzig,¹ Ferrier²) by electrical stimulation, since they do not occur after mechanical or chemical stimulation, may very well be set down to the irritation of more deeply seated regions, for the latter are unavoidably exposed to the diffusion of currents. This explanation is especially probable in the case of Ferrier's experiments. According to the results obtained by the observers just mentioned, the anterior parts of the cerebral cortex in particular are connected with the motor arrangements. Experiments with destruction of small parts of the cortex by excision (Fritsch and Hitzig), or by cauterisation by means of injections into the tissue (Nothnagel,³ Fournié), resulted for the most part in abnormal postures and movements of individual members, which are attributed (Nothnagel) to loss of muscular sense. No results as to the nature and distribution of the functions of the cortex, even of the value of approximations, can be deduced from these experiments.

It has of late been thought possible to establish by the method of experiment relations between individual regions on the surface of the hemispheres and (particularly motor) regions on the periphery.

¹ Fritsch u. Hitzig, *Archiv. f. Anat. u. Phys.* 1870.

² Ferrier, 'Localisation of Function in the Brain,' Croonian Lecture, 1874, Abstract. *Proc. Royal Society*. 'Experiments on the Brain of Monkeys,' first series. *Proceed. Royal Soc.* 1875, p. 161. 'Experiments on the Brain of Monkeys,' second series, Croonian Lecture. *Phil. Transact.* 1875, vol. ii.

³ Nothnagel, *Virchow's Archiv.* Vol. lviii. p. 420.

1. *Experiments by Stimulation*.—Whilst formerly it was surmised that the cerebral cortex was unexcitable by any of the general nerve stimuli, it has recently been found that *electrical* stimulation of localised areas on the cortex of the fore-brain occasions definite movements on the opposite side of the body (Fritsch and Hitzig, Ferrier). As, however, mechanical and chemical stimulations are always without effect, the possibility remains that the phenomena observed are due to simultaneous stimulation of deeper parts due to conduction of the current. That such excitable motor parts are present in the deeper parts of the brain is proved partly by the fact that experiments by stimulation lead to the same results even after removal of the cortex (H. Braun, Hermann¹), partly by direct stimulation experiments in the vicinity of the corpora striata (Hitzig, Burdon-Sanderson²).

2. *Experiments by Extirpation*.—After destruction of portions of the cortex by excision (Fritsch and Hitzig), by caustic injections (Fournié, Nothnagel), by washing the brain matter away by a stream of water (Goltz), phenomena set in whose extent and significance is disputed. According to some, when the destruction affects the previously-mentioned areas, the phenomena consist of disorders of the innervation of the muscular region concerned (displayed specially by awkward movements of the limbs implicated), which have been referred to affections of the muscular sense or of the act of will (Hitzig, Fritsch); according to others there occur, wherever the lesion be situated, defects in sensation as well as in movement (Goltz). All results of extirpations gradually disappear, so that one is obliged to surmise the existence of an indirect sympathy existing between the deeper regions and the surface of the cortex. In any case the question as to whether individual areas on the cerebral hemispheres are to be looked upon as establishing a connection between the mind and individual groups of muscles, or whether others are to be looked upon as organs concerned in perception, must be considered as altogether undecided.

The results of electrical stimulation of the cortex in dogs are the following (Fritsch and Hitzig):—Within the arch circumscribed by the four primitive convolutions and the *sulcus cruciatus* is situated a spot the excitation of which causes contraction of the cervical muscles; on the side of the bend is a spot connected with the *extensors* and *abductors*. Somewhat behind is one for the flexors and rotators of the anterior extremity, and on the posterior limb of the bend is a spot connected with the flexors of the posterior extremity. On the posterior limb of the third primitive convolution is an area related to the muscles supplied by the facial nerve, and in the immediate vicinity one for the eye muscles. Even in the case of other mammals, and in the frog, similar areas have been found; in man they are surmised to exist from pathological data and from experiments upon monkeys. It is questionable whether narcotics and the condition of apnoea abolish the results of stimulation, and upon this depends very much the question whether these results of stimulation are to be looked upon as reflex acts (Schiff).

¹ Hermann, *Pflüger's Archiv*. 1875. ² Burdon-Sanderson, *Proc. of Royal Society*. 1874.

In the case of newly-born animals stimulation of the cortex is without result, whilst deeper stimulation occasions movements (Soltmann). Lately, even circulatory and intestinal actions have been surmised to occur as the results of stimulations and extirpations of the cerebral cortex, especially changes in the pulse (Schiff), changes in the calibre of vessels and in the temperature of the skin (Eulenberg and Landois, Hitzig), movements of the viscera (Boche-fontaine), changes in the secretions (Lépine), hæmorrhages, &c. All these facts require further research.

We must not omit to mention that there exists in rabbits, in the neighbourhood of the posterior apex of the hemisphere, a spot on injuring which violent but transitory forward and sideward movements result after some time (Nothnagel). In this case it would seem that the movements were due to some hallucination on the part of the animal rather than to a direct motor influence.

Direct connections of the cerebral cortex with sensory or motor nerve-fibres of the external system are rendered doubtful on the anatomical grounds above mentioned, and at most only occur in special regions. It seems more probable that the same apparatuses are made use of in the production of conscious sensation and voluntary movement as in the production of reflex acts of a lower or a higher order. As in the latter motor nerve-centres are so combined that the muscles co-operate in orderly manner to cause reflex action, so it is possible that in orderly voluntary movements also these co-ordinating systems are brought into activity *as a whole*, whereby the mind is, as it were, spared much labour. This is rendered all the more probable as we cannot voluntarily contract each individual muscle alone. It is probable that the mental organs are provided not only with inciting fibres, but also with inhibitory fibres, for these centres. Whether intermediate apparatuses, concerned in similar influences exerted on the organs of the mind, are present in the case of centripetal excitations also, is still more doubtful, and such would, at least, be far less intelligible.

In addition to the above-described purposive co-ordinations of movements there exist others, which might be described as defects or weaknesses; in contradistinction to 'co-ordinated,' these are called 'associated' movements, to the category of which belongs, *e.g.* the wrinkling of the skin of the forehead during strong bodily (or mental) excitement. It is possible to render oneself, by an act of will, temporarily and, by frequent repetition, permanently, free from these 'movements of association,' as is shown in the independence of the two hands of a pianist.

Sensations in the region of other fibres than those which have been objectively excited are called 'associated sensations.' One illustration has already previously been given (p. 413), viz. the phenomenon of 'Irradiation,' or the apparent implication in stimulation of regions which were not themselves excited, in the neighbourhood of an excited cutaneous nerve-fibre, which is owing to the various connections of the grey substance of the cord. In other cases remote fibres also may appear to the mind to have been stimulated, probably because of the closeness of the stimulated and the non-stimulated fibres at their origin in the grey substance; for example, the sensation of tickling in the

larynx which follows when the external auditory meatus is touched near the tympanum, both regions being supplied by the vagus. 'Irradiation' also may be diminished by practice, as shown by the more acute perception of the touch (due to the diminution of the areas of sensation) in blind persons.

Time occupied by Psychical Processes.

1. *Reaction Period.*—By means of the method described on p. 345, and similar contrivances, the rapidity of certain simple psychical processes may be determined. In these experiments (Donders, De Jaagrr) it appeared that a signal prearranged to be given on a certain stimulation occurred later, the more complicated the psychical operation which was necessary for the production of the signal, and that, in addition, the time varied according to the way in which the stimulus acted. For example, as a means of experiments, (1) the time which elapsed between a cutaneous stimulus and the giving of a signal, which had to be varied by the person experimented upon according as the one or the other of two localities of the skin had been stimulated (*i.e.* decision had first to be made as to which of the localities had received the stimulus), was 0·086 sec.; (2) when light was used as a stimulus, *a*, decision between two colours took 0·122–0·184 sec., *b*, decision between two letters of the alphabet took 0·166 sec., *c*, decision between five letters took 0·170 sec., the signal consisting in pronouncing the name of the letter which was suddenly exhibited; (3) when the stimulus was auditory, *a*, distinguishing between two vowels took 0·056 sec., *b*, distinguishing between five vowels took 0·069–0·088 sec., the signal consisting in repeating the name of the vowel.

2. *Recognition of Objects.*—If objects be allowed to act upon the eye for only a very short time, they are not recognised; the time during which the eye must be stimulated in order to ensure recognition is, for large letters, about 0·0005 sec., and it is longer the smaller the object and the less it differs from the ground on which it rests. If a second object is presented to the eye immediately on the disappearance of the first, the first must be observed for a longer time in order to be recognised, and the longer according as the second object is a more powerful stimulus, and as the first object is more complicated in form (Helmholtz and Baxt). If, prior to the momentary illumination of an object, the attention be directed to a certain part of it, that part is perceived even though, without having the attention so directed, the illumination would be of too short duration for it to be possible (Helmholtz).

Psycho-Physical Laws.

As it is impossible to define the nature of consciousness, there exists, of course, no measure applicable to it. Nevertheless in recent times, in the more exact consideration of those states of consciousness which are most accessible to investigation, *viz.* the sensations, a method of measurement has, by an artifice, been introduced. By this method a definite relationship appears to have been established between the increase of the state of excitation of the mental organ and the increase of the state of consciousness (sensation). It must not be overlooked, however, that between the material process in the organ of sense and that in the organs of mind there intervenes a whole series of *liberations*, concerning the relations of which nothing is yet known; we are, therefore,

entirely ignorant as to where to localise this relationship, which has been termed 'psycho-physical' (Fechner¹).

These psycho-physical discoveries were made by determining the slightest increase of stimulus which was perceptible as a sensation, i.e. the increase of stimulus which occasioned the smallest possible increase of sensation. The increase of stimulus is within certain limits *constantly proportional to the strength of stimulus already applied* (E. H. Weber²), i.e. 'the stronger the stimulus (as, for instance, a pressure) already in action, the more must it be increased, in order that the increase may be perceived.' This law holds true in the case of all the organs of sense (Fechner, Volkmann). It follows therefrom that *sensations increase proportionately to the logarithms of the strength of the stimulus* (Fechner).

[*The Fundamental Formula of Fechner.*]—If β represent a stimulus, γ the sensation which corresponds to it, $d\gamma$ the smallest perceptible increase of sensation, and $d\beta$ the increase of stimulus necessary to produce that increase of sensation, then, according to Weber's law, $d\gamma$ is not proportional to the absolute increase of stimulus $d\beta$, but to the relative increase of stimulus, measured according to the strength of stimulus β , i.e. to $\frac{d\beta}{\beta}$. Therefore if k be a constant

$$d\gamma = \frac{k \cdot d\beta}{\beta}.$$

[In investigating the general applicability of Weber's law to the case of all the organs of sense and to ascertain the relation between the intensity of the stimulus and sensation in the case of each, the following methods of investigation have been employed³:—1. *The method of smallest perceptible differences*, which consists in passing from one intensity of stimulus to another until a perceptible difference in sensation resulted. Thus, in determining the smallest perceptible difference in weight which could be estimated by the hand, equal weights would be placed in the two hands and then the load in one hand would be increased until a difference in weight was just perceptible. This was the method first employed by Weber. 2. *The method of correct and false judgments*, in which two stimuli which differ in intensity are made to act many times in succession upon the organ which is being investigated, and the judgment arrived at noted. In proportion as the difference in the intensity of the stimulus becomes greater will the accuracy of the judgment increase and the number of correct as contrasted with incorrect conclusions be increased. It is concluded that the increase in stimulus bears the same ratio to the initial intensity of the stimulus when the proportion of correct to incorrect judgments remains the same. 3. *The method of mean errors*. A stimulus is made to act upon a sensory organ until the sensation which it occasions is apparently exactly equal to that produced by a stimulus of known intensity; the observation is repeated many times, and the *mean error* ascertained. This error may, by suitable treatment, be resolved into a constant and variable error, the former of which depends upon

¹ Fechner, *Elemente der Psychophysik*. 2 vols. Leipzig, 1860. [The student who is anxious to enter upon the study of the psycho-physical laws is strongly recommended to read at least the more fundamental and elementary parts of this masterly work. He will be very much aided in his studies by the careful perusal of the eighth chapter of Wundt's *Grundzüge der physiologischen Psychologie* (Leipzig, 1874), under the heading 'Intensität der Empfindung' (pp. 282–314).]

² E. H. Weber, *Wagner's Handwörterbuch der Physiol.* Vol. iii. part ii. p. 559.

³ Fechner, *Op. cit.* Vol. i. p. 71 et seq.

the various unknown physiological conditions, and the latter of which is always a certain fraction of the initial stimulus.

By pursuing these three methods various observers have obtained the following numbers, which represent the relations which must exist between two stimuli in order that a difference in sensation may be perceived in the case of different senses:—

Tactile sensations	$\frac{1}{3}$
Temperature	$\frac{1}{3}$
Sound	$\frac{1}{3}$
Light	$\frac{1}{100}$

[The ‘Measure’-formula of Fechner.]—If the equation $d\gamma = \frac{k d\beta}{\beta}$ be integrated, the sensation γ being considered as a sum of numerous small increases of sensation, then

$$\gamma = k. \log. \text{nat. } \beta + \text{const.}$$

If the constant of integration be so chosen that when $\gamma = 0$ β is equal to b —that is to say, if b is the intensity which the stimulus must already have in order to be perceived (‘liminal’ intensity, ‘Schwellenwerth’ of Fechner)—then

$$\gamma = k (\log. \beta - \log. b) = k \log. \frac{\beta}{b}$$

which expresses that γ commences to be positive when $\beta > b$. The formula for γ (the ‘Maassformel’ of Fechner), which becomes valid for every logarithmic system by changing the value of k , therefore, shows that sensations increase with the logarithms of the stimulus (considered in relation to the ‘liminal intensity’), and shows that, in general, with increasing stimuli the sensations (corresponding to the logarithms) increase, at first quickly, and then more and more slowly.

[‘One can easily observe that the relations between the increments $d\gamma$ and $d\beta$ in the fundamental formula correspond to the relations between the increase of a logarithm and the increase of the number to which it corresponds. For as one can easily convince oneself, either from theoretical considerations or by examining tables of logarithms, logarithms do not increase to an equal amount when the numbers to which they correspond increase equally, but only when the relative increase is the same; or, in other words, the increase in the logarithms of numbers remains the same when the relative increase in the numbers remains equally great.

Number.	Logarithm.
10	1,000000
11	1,0413927
100	2,000000
110	2,0413927
1000	3,000000
1100	3,0413927

By an examination of the above numbers with their corresponding logarithms, we observe that the addition of 1 to 10 leads to as great an increase in the logarithm as the addition of 10 to 100 and the addition of 100 to 1000. In these three cases the logarithmic increase is 0,0413927.’¹]

The resistance which was (p. 481) assumed to be offered by the grey network of the spinal cord, and the magnitude of which determines the extent of

¹ Fechner, *Op. cit.* Vol. ii. part 11.

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the circle of irradiation (p. 488), may, with the aid of certain hypotheses, serve as the starting-point of another deduction from Fechner's formula.

If it be assumed (1) that the resistance is so constituted that in being propagated the excitation is constantly diminished by an equal fraction of its own value; (2) that the imperceptible value which it finally attains is equal to the *liminal intensity* of the stimulus; and (3) that the intensity of the sensation is proportionate to the magnitude of the area of the circle of irradiation—the same relation between strength of stimulus, liminal intensity, and intensity of sensation is found as is expressed by 'Fechner's formula' (Maassformel). On the other hand, the empirical determination of Fechner's formula may, by Weber's law, serve for the verification of the above assumptions. It is thus at once found that k in Fechner's formula is inversely proportional to the central resistance (Bernstein).

Recently psycho-physical laws have been advanced which differ from the law of Weber and Fechner. If it be assumed that the operating stimuli add themselves so as to have the value of constantly acting but non-perceptible a , Weber's law would become

$$d\gamma = k \cdot \frac{d\beta}{a + \beta}, \text{ by integrating which it follows}$$

$$(\gamma = 0 \text{ and } \beta = 0) \gamma = k \cdot \log. \frac{a + \beta}{a} \text{ (Delbœuf);}$$

in this case the liminal intensity of the stimulus is the persistent stimulus a , and every objective stimulation would be perceived.

Another equation has been deduced from the fact that the perception of the degree of depth of two grey tones does not vary when their illumination changes; hence $\gamma = a \cdot \beta^c$, a and c being constants (Plateau).¹

Sleep.

In the mental organs two states, the physical difference between which is not understood, hold alternate sway with a certain regularity; these are the waking and the sleeping states. There appears to be a kind of sleep in which no mental action whatever takes place, so that the only central organs in operation are those of an automatic and reflex nature. The functions depending upon the central organs of this character, viz. circulation, respiration, secretion, digestion, &c., go on as usual. The reactions to external stimuli which still manifest themselves, and which proceed exactly like those of animals whose cerebra have been extirpated, must be regarded simply as undisturbed orderly reflex movements; for, as was explained on p. 479, we have no grounds for regarding them as the results of still remaining mental activity, having its seat either in the cerebrum or perhaps in special mental organs (as of the spinal cord, &c.) not in the sleeping state.

Whether states of consciousness or mental operations occur

¹ [Recently several attacks have been made upon the psycho-physical laws of Fechner, as by Professor Hering (*Zur Lehre von der Beziehung zwischen Leib und Seele I., Ueber Fechner's psychophysisches Gesetz*), and in England by Mr. Coutts Trotter (note on Fechner's law. *Journal of Physiology*. Vol. i. No. 1). A full account of all the literature bearing on this subject, and an answer to a majority of his objectors, will be found in Professor Fechner's *In Sachen der Psychophysik*, Leipzig. 1877.]

during sleep can only be decided by one means, that of the memory. From it we learn that incomplete mental actions do very frequently take place in the form of *dreams*. These are marked by sensations without objective causes (hallucinations), volitions without effect (disappointments in intended but impossible movements), and processes of thought with the usual logic of the waking state (apparent solutions of problems which seem afterwards when remembered to be absurd). No means exist of determining the duration of dreams. An observation which has frequently been made leads to the belief that possibly most dreams occur only at the moment of awakening or, at least, at the moment of a sudden and momentary release from sleep; for a dream often ends with a sensation occasioned by some objective cause which, at the same time, brings about the awaking of the sleeper. Hence the fact that extraordinary delusions as to time are an accompaniment of dreams.

Awaking from sleep appears for the most part to be caused by sensations which must be stronger the deeper the sleep. The depth of sleep may be expressed by Fechner's formula given above, by making the liminal intensity b (*i.e.* the value which a stimulus must have in order to induce a state of consciousness) so great that γ becomes negative on ordinary stimulations. Direct measurements have shown (Kohlschütter) that b , and consequently the intensity of sleep, increases from the commencement of sleep, at first quickly, then more slowly, until about the end of the first hour, after which it again diminishes, at first quickly, and then very slowly, reaching its usual value at awaking-time. Frequently, and without any apparent cause, sleep becomes suddenly less intense, relapsing again to its former depth. As a general statement, the deeper the sleep the longer it lasts. The deeper the sleep, and the greater, therefore, is b , the stronger must be the stimulus β which is requisite to call forth a sensation and cause awaking.

The chief condition of sleep is the removal as far as possible of all stimuli: hence the stillness and darkness of night are conducive to sleep. Sleep, moreover, seems to come more readily and to be deeper the greater the preceding exertions of the mental organs. During sleep the mental organs are restored to vigour, and the exhausted muscles, which are for the most part relaxed during its continuance, become refreshed. The numerous and well-known phenomena of sleep and dreaming may be passed over without further comment. Concerning the material changes in the brain during sleep, the alterations of blood-pressure, nutrition, &c., we have as yet mere hypothesis unsupported by facts.

APPENDIX.—*Circulatory and Nutritive Conditions of the Brain and Spinal Cord.*—The activity of the central organs is dependent in a high degree upon their blood-circulation, as shown by the consequences—*anæmia*, *hyperæmia*, *stagnation*, &c. Special arrangements appear to exist with a view to regu-

late the blood-pressure. As such may be mentioned: 1. The fact that brain and spinal cord are enclosed in a bony case which they, together with the cerebro-spinal fluid, completely fill. On account of the incompressibility of these parts, and of the unyielding nature of the enclosing case, cardiac and respiratory variations in the vascular areas appear to be impossible. In order that such variations should occur, either the case must be opened (thus, the brain shows respiratory pulsations when the skull is opened; and a manometer communicating with the interior of the cranium exhibits respiratory and cardiac oscillations) or the cerebro-spinal fluid must flow out (thus, in injuries to the spine, the brain shows respiratory movements which, as it seems, induce basilar meningitis by friction, Rosenthal). Artificial or pathological increase of intracranial pressure causes much disturbance of function, presumably depending upon circulatory mischief. 2. The brain, by means of the circle of Willis, is secure from any sudden interruption to circulation by the closure of an artery. 3. Changes of blood-pressure in the brain, which might result from sudden changes in the position of the body (as, for instance, on rising from the horizontal position), are said to be prevented by the thyroid body which forms a collateral blood-reservoir (Liebermeister). If the change of position occurs too suddenly a transitory faintness follows. The thyroid body is said to regulate blood-pressure in the brain in another way also, since, when swollen by the strong influx of arterial blood, it compresses the carotid (Guyon); that is to say, when the muscles are powerfully excited, the carotids sometimes exhibit no pulsation (Maignien). 4. The vaso-motor nerves of the brain, which traverse the highest cervical ganglion, but do not wholly lie in the sympathetic cord (Nothnagel), are the media for the general regulatory influences.

3. Sympathetic Centres and Nerves.

In general those nerves are described as sympathetic, irrespective of their origin, which supply the viscera and the vessels. Moreover, the non-medullated nerve-fibres, which are present in such large numbers in sympathetic nerves, are called 'sympathetic fibres.' The origin of these sympathetic fibres is not exactly determined. The numerous ganglion-cells which are aggregated in the large somatic cavities, or are scattered singly through the parenchymata of many viscera, are to be regarded as the principal central organs of the sympathetic system; but it has been shown anatomically and physiologically that many sympathetic fibres are in communication with the cerebro-spinal organs, partly by means of the rami communicantes of the spinal nerves, and partly by means of unions formed with the cranial nerves. This communication has been already alluded to in the description of the oculo-spinal centre (p. 498) and of the origin of the vaso-motor nerves (p. 497). Nevertheless no sympathetic nerve has ever been proved to be in connection with the will, for all the movements of the viscera are completely *involuntary*. The sensibility of the viscera, also, is so extremely slight that it is supposed to be due to the few medullated ('cerebro-spinal') fibres which the sympathetic nerve-trunk contain. Smooth muscles are regulated only by sympathetic fibres, and hardly any instance is known of other descriptions of muscles being supplied from this system of nerves.

The question as to the position of the ganglia, which are scattered throughout the sympathetic nervous system, is a peculiarly difficult one; the ganglia occur partly as parenchymatous ganglia, connected with the peripheral terminations, partly as ganglia situated in the course of, the sympathetic cord, or imbedded in the plexuses contained in the visceral cavities; even the ganglia on the roots of the spinal nerves are generally accounted to belong to the sympathetic system. Even the structure of those organs is disputed, it being not always certain whether the cells which they contain are uni-, bi-, or multipolar, or even apolar.

That central functions belong to these organs cannot, however, be doubted. 1. On account of the analogy with the ganglion cells of the brain and spinal cord. 2. Because after destruction of the brain and spinal cord the visceral ('vegetative') functions persist for a long time (Bidder), e.g. the movements of the separated heart, &c. That central functions have not been ascertained in the case of many sympathetic ganglia, affords no ground for a general denial of such a function. It is generally surmised that sympathetic ganglion-cells constitute *scattered central organs connected with motion and secretion*, which in part act automatically (in a rhythmical or tonic manner), in part act reflexly, their automatic actions being in great part under the regulating influence (retarding, inhibiting, &c.) of nerves which take their origin in the brain or spinal cord.

The functions of the sympathetic central organs are, as far as is known, the following: 1. To subserve reflex action, which, so far as muscular movements are concerned, is of the purposelike, orderly character previously described; hence co-ordinating arrangements must exist in connection with them. In addition to motor reflex actions we get also secretory. 2. To subserve automatism (motor and secretory). Possibly many of these apparently automatic excitations ought to be classed as reflex: the cerebro-spinal organs cannot be concerned in such excitations, as the functions ('vegetative') which really depend upon the sympathetic system continue for a long time after destruction of these organs (Bidder). In the case of automatic, as of reflex, actions, co-ordinating arrangements are recognisable. The rhythmical automatism in sympathetic nerves is under the regulation of inhibitory and accelerating fibres, just as was the case with nerves of the cerebro-spinal system.

The following may be taken as a more particular statement of the functions of the sympathetic organs:—

1. *The Ganglia of Parenchymata.* Many organs contain in their substance ganglion-cells, by means of which their functions are in part regulated. Such organs are especially the heart, and, according to most authors, the stomach, intestines, uterus, &c. The ganglia of the heart are most easily studied. They possess a

rhythmical automatism in virtue of which isolated fragments of the heart pulsate of themselves. In addition, co-ordinating arrangements are present whereby the various segments of the isolated and uninjured viscus contract in regular sequence. Moreover, the rhythm is under the control of accelerating and retarding fibres, both of which sets arise from the cerebro-spinal organs, but the former of which run in sympathetic courses (*viz.*, through the lowest cervical and uppermost thoracic ganglia), while the latter pass along the vagus. The customary assumption that the heart also contains (in the auricle) *inhibitory central organs* is doubtful.

The stimulus which produces automatic excitation of the cardiac ganglia is unknown. In the frog's heart it appears to be the oxygen of the air or of the blood, since regular pulsation ceases on excluding the oxygen (Goltz, Cyon) although direct stimulation still induces contraction, the muscles themselves, therefore, remaining irritable. On the other hand, the presence of carbonic acid appears to excite the inhibitory system (Traube, Cyon). In the case of mammals the conditions are more difficult to grasp, as it is impossible to experiment with the isolated heart.

Intestinal peristaltis affords another example of automatic co-ordinated movement brought about by parenchymatous ganglia. In this case also an inhibitory mechanism (for the small intestine) is found in the splanchnic nerves, while it would seem that accelerating fibres reach the intestine from the sympathetic plexuses of the abdomen. The stimulus for this automatism is also unknown.

The presence of air increases the movements, as does also an increased venous condition of the blood, caused, for example, locally by stagnation.

Concerning the innervation of the uterus Chap. XII. may be consulted.

2. *Ganglia, Plexuses, and Sympathetic Cord.* Nothing is known about the action of the numerous ganglion-cells found in these structures. Experiments in which stimulation and section have been made use of have merely led to a knowledge of the fibres, derived apparently from the cerebro-spinal organs which chanced to pass through them. The only apparently established fact indicating the existence of reflex powers in a ganglion, *viz.*, the secretion of saliva induced in a reflex manner through the sub-maxillary ganglion, has recently been doubted (Eckhard); for the result follows on electrical stimulation only, and may be due to a diffusion of the current, which may thus affect the secreting nerves themselves.

In the cervical portion of the sympathetic the following fibres have been shown to exist:—

1. Vaso-motor fibres for the corresponding half of the head: ~~these~~ have their origin in the cerebro-spinal organ.

2. Fibres for the dilatator pupillæ: these also take origin in the cerebro-spinal organ.

3. Fibres for the smooth orbital muscle of Müller, and also, apparently, for the rectus externus muscle, since section of the cervical sympathetic induces internal strabismus.

4. Secreting fibres for the salivary glands, and for the lachrymal glands: the origin of these is unknown.

5. Accelerating fibres for the heart (von Bezold).

6. The lowest cervical ganglion, besides the highest thoracic ganglion (*ganglion stellatum*), with which it is frequently united, conducts accelerating fibres to the heart through the third branch of the ganglion (E. and M. Cyon); the first and second branches are the roots of the depressor nerve.

7. Fibres proceeding to the cerebro-spinal organ which call into activity the cardiac inhibitory mechanism.

8. Fibres proceeding to the cerebro-spinal organ, which stimulate the vaso-motor centre (pressor fibres).

In the thoracic portion of the sympathetic but few clearly established experimental results have been obtained. The superior thoracic ganglion (*ganglion stellatum*) conducts to the heart accelerating fibres, which reach the ganglion by way of the cervical sympathetic cord (von Bezold) and the root accompanying the vertebral artery (von Bezold and Bever).

The plexus cardiacus, belonging to this part of the sympathetic system, is constituted of fibres passing to and from the heart and belonging to the vagus, depressor, and sympathetic nerves. In the thoracic portion also arise the splanchnics, major and minor, to which the following fibres may be assigned (spl. major): 1. Inhibitory fibres for the intestine. 2. Accelerating fibres for the intestine (surmised from the effect of post-mortem stimulation). 3. Fibres inhibiting the renal secretion. 4. Vaso-motor fibres for the extensive vascular region of the abdomen. 5. Centripetal fibres which inhibit the heart in a reflex manner (situated in the frog in the sympathetic cord) (Bernstein). 6. Fibres, irritation of which causes an abnormal appearance of sugar in the urine (von Gräfe, Eckhard, Ploch).

Concerning the abdominal portion of the sympathetic we have but few trustworthy statements. Irritation of the cord and the plexuses (coeliac, mesenteric, renal, suprarenal, spermatic, hypogastric) causes for the most part movements, or increased movements, of neighbouring organs, viz., intestine, bladder, ureters, uterus, vesiculæ seminales, and spleen (induced in the last-mentioned organ, by irritation of the plexus lienalis, a branch of the coeliac plexus, Jaschkowitz). Section or extirpation of the sympathetic cord and plexuses cause chiefly circulatory and nutritive disturbance. It may be mentioned that extirpation of the coeliac ganglia

produced, in one well-established case, a disturbance of digestion, in which undigested food was voided *per anum* (Lamansky).

The discoveries which have been made concerning the uterus will be given in Chap XII., when considering parturition.

The suprarenal capsules are very rich in nerves and contain in their interior cells resembling ganglion-cells; on this account their function has been supposed to be nervous, but this is as yet unsupported by facts. Other suppositions as to their nature have already been stated on p. 211.

PART IV.

ORIGIN, DEVELOPMENT, AND DEATH OF
THE ORGANISM.

CHAPTER XII.

A. GENERAL OBSERVATIONS.

THE origin of new organisms is always associated with the existence of others which have preceded them. Since the belief in the free formation of cells has been almost universally abandoned, one may affirm that no organic form originates in shapeless matter, but that each form is derived from a pre-existing one. The general plan of new formation is either a decomposition of an organism into parts which henceforward develop independently, or the separation of a part which develops individually from an older organism which continues to exist; the new part may either remain in connection with the old or may separate from it.

The doctrine of *spontaneous* or *equivocal generation*, which ever finds defenders—the doctrine which affirms that organised beings do spring from shapeless matter, as in fermenting or decomposing fluids—is opposed to the statements made above.

The apparent proofs of such spontaneous generations are:—

1. The development of vegetable and animal organisms (fungi, infusoria) in infusions of organic substances.

2. The development of organisms (entozoa) within completely shut cavities. In both cases, however, the organisms spring, as may be proved, from the numerous germs contained in the air; as the infusion remains barren if the air reach it without any germs (these being separated by filtration from it), or if the germs contained in the air be destroyed before it reaches the infusion, as by conducting the air through red-hot tubes. The development of entozoa is unquestionably due to the germs which are introduced with the nutriment, and which can in certain stages of their existence wander into the closed cavities of the body.

Notwithstanding what has been said in opposition to the present occurrence of spontaneous generation, science teaches us that the temperature of our globe was once so high that no organised being can have existed upon it, so that at some period in its history a true primordial generation must have taken place.

The resemblance between the parent organism and its offspring not only extends to the general form, but to peculiarities of formation, which characterize not merely the *genus*, or the *species*, but even the *variety* or *race* to which

it belongs, so that peculiarities in form which have arisen accidentally can easily be transmitted.

This constitutes the basis of the attempt to explain the origin of species and genera through inherited and ever-increasing varieties in form (Darwin). In order to explain the fact that a variety in form, once present, develops further and further, an assumption suffices, upon which the Darwinian theory is based, viz. that of all existing organisms only a fraction meets with the conditions necessary to continued existence, and that consequently a struggle for existence is going on amongst living beings. In this struggle those beings will always be the conquerors which are endowed with properties which render them adapted to the local conditions in which they are placed. If, therefore, in any animal species a certain variety of form has arisen, which renders the individuals concerned more suited to the existing conditions than their fellows (as, e.g. more able to procure nourishment, to bear particular temperatures, to vanquish foes, to allure the opposite sex for purposes of reproduction), then these individuals will, under the given circumstances, hold the upper hand in the struggle for existence, their peculiarities will be maintained by inheritance, and by further variation in the same direction will establish a wider and wider separation from the original form. In this way it is possible that from the same stock there may be developed in different localities such deviations that out of varieties there may spring new species, and out of species new genera.

The inability to discover the transition-forms between two species is easily seen to depend upon the fact that, of all the forms which result from one stem, the extreme forms least of all come into collision in the struggle for existence, whilst the mean forms most easily are destroyed in the process.

By carrying the same principle further, but in an opposite direction, the surmise is formed that all animal (and vegetable) forms spring but from a few, perhaps even from a single parent form. The Darwinian hypothesis has, also, another fruitful side, in that it destroys specially all teleological speculations, by showing that of all possible forms which can exist, only those most adapted to their uses can survive, whilst the others must succumb.

Seeing that in the breeding of animals the heritability of certain peculiarities is taken advantage of, and these peculiarities are thereby further developed, the individuals which possess them in a pre-eminent degree being specially cared for and employed in propagation, the principle above alluded to has by its expositor been denominated '*natural selection*.'

Forms of Reproduction.

The fundamental forms of reproduction are the following:—

1. Fission of the existing organism into several pieces (of equal value), which continue to live independently, either united or separated, and which grow to the size of the original organism. This is spoken of as the *fissiparous* mode of reproduction. Closely connected to this is the separate continued existence of the pieces of animals which have been artificially divided, and which has often been observed.

2. Scission of a constituent part of the parent organism. The constituent part may either remain joined to the parent or may separate from it; in either case it develops independently of it, whilst the parent continues to exist. If the part which separates is an important multicellular constituent of the parent organism which remains united with it for a time or for ever, the process is termed '*gemmiparous* reproduction.' If, however, the separating

portion be but a single cell, which develops independently of any connection with the parent organism, the process is termed '*oviparous* reproduction,' and the cell concerned in this process is called 'germ-cell,' or 'egg,' or 'ovum.'

The fissiparous and gemmiparous modes of reproduction only occur in the lowest animal forms. The oviparous mode, on the contrary, occurs throughout the rest of the animal kingdom, even in man, and in many of the lower animals in addition to the first-named processes of reproduction.

The ovum is the product of a special organ, 'the ovary.' It is only in a few animals that the development of the egg proceeds alone to the very end ('*parthenogenesis*').

In order that development may occur, or at any rate proceed, beyond a certain limit, the egg requires, as a rule, contact with a peculiar element. The peculiar element is '*semen*,' the product of another organ, the 'testicle.' The ovary and the testicle are either (as in the higher animals) found in separate individuals or they are both present in the same individual. In the first case the individual furnished with the ovary is termed *female*, as distinguished from the *male*, which is provided with the testicle; in the second case the creature (as in many of the lower animal forms) is said to be 'hermaphrodite.' The contact of semen and ovum is called 'fertilisation' or 'impregnation,' and reproduction by means of eggs which have to be fertilised is spoken of as 'sexual reproduction;' the fissiparous and gemmiparous modes of reproduction, as well as parthenogenesis, constitute, on the other hand, 'non-sexual' modes of reproduction.

Undoubtedly parthenogenesis has, hitherto, only been certainly determined to occur in a few species, and in them it only occurs side by side with true sexual reproduction, and yields invariably only individuals of one sex (*e.g.* in bees and in a species of wasp, only males, in the *psychidæ* females).

The best known example, that of bees, may here be specially considered. In a bee-hive there occur three classes of individuals, viz. males (which are called *the drones*), females incapable of reproduction (*the working bees*), and one female capable of reproducing (*the queen bee*). The queen bee once in the year, in what may be termed the nuptial flight, is impregnated by one of the drones which surround her, and returns with a full '*receptaculum seminis*.' She is now in a position either to fertilise the eggs which she lays or to leave them unfertilised. Both these events occur, and they are governed by the cell in which the egg is deposited; in the cells of the drones are placed the non-fertilised, and in the cells of the working bees the fertilised eggs. The emission or non-emission of the semen which is stored up depends either upon the will (instinct) of the queen bee or upon the mechanical relations of the cell into which she thrusts the posterior part of her body.

Whether the fertilised ovum develops into a sterile female (working bee) or into a fully developed female (queen bee) depends upon the feeding of the larvæ by the working bees, perhaps also upon the form and size of the cells.

A momentary parthenogenetic development occurs in some animals, in which the non-fertilised egg goes through the early stages of development (first stages of cleavage), and then an arrest occurs; such a process has hitherto been observed in the sow (Bischoff), in the rabbit (Hensen), and in the hen (Oellacher).

Sexual Maturity. Fertility.

In the case of all organisms the conditions required for reproduction first occur at a particular stage of their development, generally only when their growth is completed, so that the excess of 'the receipts' over 'the expenditure' of the body which has hitherto served the purposes of growth may thenceforward be used in the production of generative materials, or even (in the case of viviparous creatures) in the nutrition of the developing egg. It is only at this particular period (period of puberty) that in animals of different sexes the complete development of the germ-preparing organs (ovary and testicle) occurs. Henceforward, however, for long periods of time, often until death, the reproductive process proceeds, generally at regular intervals. The number of the progeny of one individual, or of one pair of individuals, *i.e.* their 'fertility,' varies very greatly throughout the animal kingdom. In making such a quantitative determination one may start from two different stand-points. If reproduction be looked upon as a function of the maternal organism in relation to other functions, *viz.* as an expenditure in relation with the other sources of expenditure and income which constitute the whole exchanges of the matter of the body, then we must determine the relation between the weight of the animal and the weight of the reproductive material yielded by it in the condition in which it leaves the body (as eggs in the oviparous, young creatures in the viviparous, semen in male animals). Such determinations (Leuckart) exhibit enormous differences in the expenditure of generative matters; thus, for example, the yearly generative expenditure of the female organism is, in the human female, about $\frac{1}{14}$ th of the body weight, in the sow about $\frac{1}{2}$, in the mouse about three times the body weight, in the hen five times, and in the queen bee 110 times the body weight. If now we consider reproduction in relation to the maintenance of the species, we must compare, instead of the weight, the number of the real progeny resulting. The first kind of determination alluded to cannot be utilised for this purpose, for, firstly, the same weight of generative material represents in different species a widely differing number of *possible individuals*; and, secondly, a great number of circumstances must concur in order that fertilisation and development should occur, and these circumstances are relatively only rarely present, so that in general only a small fractional part of the generative material really accomplishes its end.

The number of the progeny can, however, only be very rarely determined; as one may, however, venture to assume that the object of reproduction is to maintain the number of individuals of

the species approximately constant, it follows that the number of the progeny stands in a certain relation to the mean duration of life of the species. If we designate the number of years of the latter by n , the constant number of individuals by a , the number of individuals which must be born in a year will be $\frac{a}{n}$. For each individual being of the species, there will be yearly born in the mean $\frac{1}{n}$ of progeny. How much of this production falls upon each reproductive individual depends principally on, 1, whether the new creature originates sexually, i.e. by the concurrence of two parents; 2, the number of reproducing individuals in relation to the total number, as well as the duration of the period of fecundity in relation to the duration of life. The number of germs produced will, in general, exceed the numbers obtained by the above methods, the rarer are the conditions realised necessary for fertilisation and development.

Sexual Reproduction.

The egg (ovum) in its simplest form is a globular cell, the granular lecithin-containing protoplasm of which is called the yolk (vitellus). Besides this, many eggs possess a (secondly deposited) secondary yolk (Nebendotter), which occasionally consists of immigrated cells. The vesicular nucleus of the ovum is called the *germinal vesicle* (vesicula germinativa), and the nucleolus which is seen in the vesicle is called the *germinal spot* (macula germinativa). In many eggs a cell-membrane cannot distinctly be made out, and in the majority of cases the cell is found surrounded by an envelope of different form and not belonging to it, which, when a vitelline membrane is present, is deposited upon it. This envelope is in its simplest form a structureless, tolerably thick, membrane, so that seen in profile it appears as a bright ring (zona pellucida of mammalia and man). In the majority of eggs it is perforated by numerous canals; in some it is covered by villus-like processes, the most diverse forms being observed in invertebrate animals. In many animals the envelope possesses a tolerably large opening, which is of importance in the process of fertilisation, and which is called 'the micropyle' (Keber): this is especially the case in numerous invertebrata and fishes, probably also in higher vertebrata.

The chemical constituents of the yolk of the egg are principally derivations of lecithin (vitellin, ichthin, protagon (?), various albuminous bodies, a colouring matter related to hæmatoidin, an amylaceous body, salts and water.

In many cases the egg possesses accessory envelopes, which it partly brings with it from the seat of its formation in the ovary (as the *discus proligerus*; the yellow of the bird's egg is to be looked upon as the entire ovarian follicle, and only the germ-disc is the ovum proper), partly it receives on its way through the excretory passages; thus the white and the shell of the bird's egg are formed around it in its passage through the oviduct—a passage which is effected by peristaltic movements. In this way are produced the spiral twists of the *chalazæ*. The ovum of the rabbit receives in a similar manner an envelope of albumen as it passes along the Fallopian tube.¹

The liberation of the mature ovum from the seat of its formation in the ovary occurs at certain periods, the periods of *rut* or *heat*, which occur once or several times in the year; the number of eggs which are liberated at one time varies from a single one (in man) to many thousands. In general, sexual intercourse is only fruitful when taking place during the period of heat or rut.

The *semen* consists of a large number of corpuscles, which are of a form peculiar to each species, and which are suspended in a highly albuminous fluid, and which generally move through it in a particular manner. The form of these seminal corpuscles (zoosperms, spermatozoa, or spermatozoids) is similar in all vertebrata and in many invertebrata; they consist of a globular, oval, or cylindrical (sometimes corkscrew-shaped) body or head and a fine tolerably long thread or tail, which is continually engaged in a whip-like movement. In invertebrate animals numerous other, in part motionless, forms are seen.

Impregnation consists in contact of the semen with the liberated ovum. This contact happens either within the female organs of generation, into which the semen is conducted, or outside of them, by the semen being poured over the previously extruded ova, or by being accidentally brought in contact with the eggs, as by the surrounding water. Even artificial fertilisation is possible. Very small quantities of semen appear sufficient to fertilise, provided that they contain spermatozoa (Spallanzani).

The union of the male and female bodies which is required in the first-mentioned mode of impregnation is denominated sexual intercourse or copulation. In the majority of animals it occurs during the period of rut, during which time, along with the special condition of the germ-preparing organs, in both sexes the desire for intercourse, 'sexual appetite,' awakens. Probably in all animals the act of copulation is accompanied by voluptuous sensations.

The nature of impregnation is as yet unknown. In all probability it is, above all, essential, in order that it should occur, *that*

¹ According to recent researches (His) the yolk of the bird's egg consists, in addition to ovum proper (principal yolk) and the germinal vesicle and the accessory yolk, of cells of the membrana granulosa of the follicle which have wandered through the zona. In the mammalian egg, at least, only a small part of the cells of the membrana granulosa wander into the egg, the remainder forming the epithelium of the follicle and the 'discus proligerus.'

one or more spermatozoa should penetrate the ovum. At any rate spermatozoa have been found within the fecundated eggs of the most diverse species of animals. The entrance of the spermatozoa occurs, in eggs which possess a *micropyle*, probably through it, otherwise perhaps by an active penetration of the ovi-sac; both processes have been observed to occur.

The development of the embryo commences soon after the contact or penetration of the semen, being brought about, or at any rate furthered by it, in an inexplicable manner. The spermatozoa which have penetrated disappear after a short time; nothing definite is known in reference to the changes which they undergo.

Development of the Impregnated Egg.

The development of the egg begins in all cases with the formation of numerous cells, through a progressive division of the ovum; this is known as *segmentation*. Out of the cells which are formed originate the organs of the embryo in so many ways that no general principles applicable to all animals can be laid down. In ova which possess a food-yolk (birds, amphibia, fishes, strictly even mammalia) only a partial segmentation occurs, *i.e.* the whole of the yolk does not take part in the process, but only that part of it which contains the germinal vesicle, which is called the principal yolk or formative yolk. The non-segmenting food-yolk, which is derived from the granulosa cells of the follicle, undergoes no morphological changes, but it yields its chemical constituents to the embryo so as to build it up, hence its name.

The development of the ovum takes place in the majority of cases outside the maternal organism, in the most suitable localities suitable to the process. In the majority of cases a certain temperature is requisite for development, which is partly obtained by the choice of the locality in which the egg is deposited, partly afforded by the sun's heat, and, lastly, partly by the maternal body, given whilst it covers the eggs (hatching); this can also be artificially applied (artificial hatching).

The second condition necessary to development is the access of oxygen. In the developing egg, as in the already developed organism, processes of oxidation occur, which consume oxygen and yield carbonic acid. The exchanges of the gases with the atmosphere, or with the water which contains gases, takes place through porous openings. In many cases the development of the ovum takes place within the maternal organism in a dilatation of the efferent generative apparatus, *i.e.* in the uterus, as in mammalia, and in man. The two conditions requisite for development are here realised in a very complete manner; the temperature is maintained by the sojourn in the equally heated maternal body; the

respiration takes place by means of the very early developed vessels of the embryo, which form a capillary system in connection with a part of the uterine wall; the walls of the foetal capillary system come into immediate contact with the maternal capillaries, which are also strongly developed at the above-mentioned part.

At this spot—in the ‘placenta’—there occurs a passage of oxygen from the blood of the mother into that of the embryo, and of carbonic acid in the reverse direction. The same organ is the medium of the passage of nutritive matters from the body of the mother to that of the embryo. After development has proceeded to a certain point, the egg is expelled through the genital aperture, the process being denominated ‘birth.’

Modifications of Development.

The development of the ovum into a complete organism similar to the one from which it is derived does not always take place continuously. In certain classes of animals development is arrested for considerable periods at certain stages; at these stages of development the organism manifests similar functions to those which are observed when it is completely developed, viz., voluntary motion, capacity to take food, to digest, &c. This is called the ‘larval condition,’ and the best known examples are afforded by the larval stage in the ‘metamorphosis’ of insects. Even reproduction occurs in such larval conditions, by fission and budding; when this occurs the process is termed ‘alternate generation.’ As larvæ generally possess a thoroughly different form, and as their life cannot be distinguished from that of the fully formed organism, numerous larvæ have been described as separate species before their origin and further development were discovered. This has specially occurred in cases of alternate generation; the larvæ which possess the functions of a fully developed animal, including the power of reproduction, and the forms of which differ in an extraordinary degree from that which they ultimately assume, have for long periods of time been held to be distinct animal forms, even to be animals belonging to different classes or orders.

The *leaf-louse* may be cited as offering the simplest example of alternate generation. From the fertilised ova of this creature, early in the spring, non-sexual young are developed, and these produce animals similar to themselves which are born alive; the latter, in their turn, give birth to a new viviparous generation, and the process is repeated during several generations, until finally, later in the autumn, young are born which are partly male and partly female; these copulate and produce fertilised ova which remain inactive during the winter; in spring the cycle of changes again commences. The viviparous generations cannot be looked upon as composed of parthenogenetic females, because they never change into the egg-producing females of the final generation (Leuckart).

A more complete example is furnished by intestinal worms belonging to the cestode class, e.g. by tape-worms (*tænia solium*).

The living tape-worm existing in the intestine of man consists of a head with suckers and hooklets, and of a chain of segments (joints), which are smallest near the head and then grow longer and broader. The smallest are the youngest, and these originate continually by a process of budding from the so-called neck. Every joint is to be looked upon as an individual, and contains male and female organs of generation, which develop with age. Sexual congress takes place between these joints, so that the oldest always contain fertilised eggs already in a state of development. These joints (proglottides) are from time to time thrown off, and leave the body with the excrement. Presumably the ova, when they again directly reach a human intestine, can again develop into the heads of tape-worms and generate new joints; there would then be an alternation between two generations, one increasing by budding and one by a sexual process (hermaphroditic).

The usual process, however, consists in this, that the ova, previously referred to, find a host in one of the numerous animals into whose bodies they can be introduced with the food, and nearly always by preference the host, in the case of the *tænia solium*, is a particular animal species—the pig.

Here the hook-provided embryo bores its way to parts suited for its residence (the liver, the brain, the muscles, the *tænia solium* in the pig specially reaching the sub-cutaneous cellular tissue;—possibly a part of the way to the organs is travelled over by the embryo finding its way into the blood, giving rise to an embolism and being liberated again), and there develops a bladder-like appendage (cyst) into which it can occlude itself. Thus out of the *tænia solium* is formed the *cysticercus cellulosæ* of the pig (measley pork), which, when the flesh is consumed by man, reaches his alimentary canal, where, by the action of the digestive fluids, it loses its bladder and acquires joints. In other cases, as in the *echinococcus hominis* (found in the liver, kidneys, &c., and derived from the *tænia echinococcus* of the dog's intestine), there originate within a headless bladder 'acephalocyst,' which develops from the embryo, many small cysts with the heads of *tæniæ*, and within there often occur new generations.

In this case two different kinds of non-sexual, alternate with sexual, reproduction, of which the one, which can pass through many generations, is by budding from the embryo bladder, the other by budding from the *tænia*-heads.

B. REPRODUCTION IN MAN.

The propagation of the human race is effected by a sexual process of reproduction, impregnation takes place internally, and the development of the embryo being intra-uterine. Birth occurs about 280 days after the impregnation of the ovum. Usually only one ovum, rarely two, still more seldom three or more ova develop at once.

The period of sexual maturity (puberty) generally commences in man between the ages of 13 and 17, being somewhat earlier in woman than in man, and somewhat earlier in hot than in cold climates. In addition to the development of the organs of generation and their appendices (as, *e.g.*, the hair which covers the pudenda), and the display of the functions connected with this development (menstruation in women, seminal emissions in man), there appear at this period many other corporeal changes, such as the development of the mammary glands and the growth of the *panniculus adiposus* in woman, the changes in the voice and the

growth of the beard in man. At the same time there occur also certain psychical changes, and the sexual passion manifests itself.

The period of fecundity continues in woman until about 45 or 50 years of age; in man no certain limit has been ascertained to exist. In woman the close of the period of fecundity and the arrest of menstruation are associated with certain bodily changes, especially of the generative apparatus, which are 'comprehended' in the term 'involution,' but in which the normal cannot yet be sufficiently distinguished from the morbid changes.

Formation of the Ovum.

The mature human ovum is globular, and has a diameter of 0.18–0.2^{mm}. The external envelope is a tolerably thick, clear, structureless membrane, which presents the appearance of a clear ring (*zona pellucida*). No membrane has been discovered below this. The yolk is a tough granular protoplasm, probably contractile; within it, situated usually excentrically, is the germinal vesicle, presenting the appearance of a clear bladder with a dark germinal spot. The existence of a food-yolk surrounding the principal yolk is probable. The chemical constituents of the human ovum are probably those mentioned at p. 525.

The formation of the egg takes place in the Graafian follicles of the ovary; these are spherical bladders, which, when ripe, are about the size of a pea, and are imbedded in the stroma of the ovary. Their wall is composed of a vascular capsule, composed of connective tissue, which is coated on its inner surface by a stratified epithelium ('*membrana granulosa*' seu '*germinativa*'). This epithelium is at a certain spot massed into a mound of cells (*cumulus* s. *discus proligerus*), in which the ovum lies embedded. The hollow space in the follicle is filled with a yellow albuminous fluid.

According to recent researches (Pflüger, His, Waldeyer, Koster, and others) the development of ova and follicles probably takes place in mammalia and man in the following manner;—

The connective-tissue rudiment of the ovary, which is a part of the connective tissue of the Wolffian body, is covered by a layer of cylindrical cells distinct from the peritoneal epithelium; this very early growing thicker inserts itself into the simultaneously growing stroma of connective tissue. By this simultaneous growth there is formed in the ovarian stroma a cavernous system of tubes quite filled with cells (Valentin), the so-called egg-tubes ('*Eischläuche*').

Some of these cells distinguish themselves soon by their size and appearance from the remainder; these are the ovum-cells (according to Pflüger primordial eggs, which by further division form ova). Later on, the tubes separate into divisions, of which each contains one, a few several egg-cells, surrounded by the smaller cells of the granulosa; in these divisions, i.e. in the rudiments of the follicles, between the cells, there is formed a cavity filled with liquid, which extends around and divides the cells into one set which lies in contact with the wall of the follicle (*membrana granulosa*), and into another

which remains in relation with the other, but which surrounds the ovum (*cumulus proligerus*) which is now placed peripherically.

During their maturation the ova acquire their *zona pellucida* and food-yolk, both of which are presumably products of the layer of cells of the *granulosa* which lie immediately in contact with the egg (this layer is distinguished by the cylindrical form of the cells).

In cases where the food-yolk consists of cells, these are derived from the *membrana granulosa*, and have wandered through the *zona*. In the bird's egg all the cells of the *membrana granulosa* wander, and the yolk represents the entire follicle.

At determined intervals one or more of the follicles of the ovary reach maturity, *i.e.* their size and the distension of their walls increase so much, in consequence of the augmentation of their fluid contents, that they burst. As the follicles in ripening always approach the surface of the ovary, and as they lie before their rupture immediately beneath the capsule of connective tissue which invests the organ, the fluid contents, together with the ovum embedded in the cells of the *cumulus proligerus*, would be extruded immediately into the abdominal cavity. As, however, before the rupture of the follicle, the fimbriated extremity of the Fallopian tube is so apposed to the surface of the ovary that, cup-like, it embraces the follicle, the ovum enters the canal of the Fallopian tube, and is impelled through it into the uterus by the outwardly directed movements of the cilia of the epithelium which lines the tube.

The process of liberation of the ovum is associated with a capillary hæmorrhage from the uterine mucous membrane, which constitutes the phenomenon of 'menstruation.' The liberation of ova occurs in woman during the whole period of her sexual life, except during pregnancy and lactation, at intervals of twenty-eight days, the hæmorrhage continuing for several days. Usually only one ovum is extruded at a time; rarely two or more are liberated.

In mammalia the liberation of ova (rut or heat) occurs more seldom, *viz.* once or several times in the year, but in them several ova are generally thrown off within a short period: in their case, too, a discharge of blood takes place from the organs of generation.

The object of the hæmorrhage appears to be to stimulate the uterine mucous membrane, so as to favour the reception of the ovum in the event of its being impregnated (Pflüger). In support of this view may be cited the fact that, in animals which possess several placental sites, at the time of 'heat,' blood merely exudes from those sites.

The broken and emptied Graafian follicle, which, at most, contains a drop of blood which has entered it during the process of rupture, undergoes special changes, some of which commence before the rupture. The cells of the *membrana granulosa* increase first, and become filled with a yellow fat, whilst the

capsule becomes less and less distinguishable from the stroma of the ovary.

Thus originates the *corpus luteum*, which progressively recedes into the interior of the ovary. After it has attained a certain size (generally before the commencement of the succeeding menstruation, for one generally finds but one corpus luteum in the ovary) it shrivels into a cicatrix, which soon becomes imperceptible, and which sometimes contains crystals of hæmatoidin, which are derived from the extravasated blood. At the place where the ovarian capsule was broken there also remains a cicatrix, so that, as life advances, the originally smooth surface of the ovary becomes more and more puckered. During pregnancy the last formed *corpus luteum* is developed much more slowly, and reaches a much greater size, so that before the periodical liberation of ova was known such were alone spoken of as 'corpora lutea vera.'

The blood which is separated during menstruation is mixed with uterine mucus, with epithelium cells, and mucous corpuscles; it is probably to this admixture that the menstrual blood owes its decided alkalinity, and its inability to coagulate.

The processes which go on during menstruation are yet, in many respects, obscure; no sufficient explanation has yet been given of the cause of the periodic maturation of the follicles, nor of its relation to the external hæmorrhage, nor of the peculiar course which the follicles follow in the ovary before and after their rupture, but especially concerning the mode in which the apposition of the Fallopian tube to the ovary takes place. The discovery of specially arranged unstriped muscular fibres in the fold of peritoneum which supports the uterus, the Fallopian tubes, and the ovaries (Rouget) appears to offer an explanation for the majority of these phenomena. These muscular fibres must, in the first place, bring about the apposition of the orifices of the tubes to the ovary, and in the second place, by compressing the venous trunks, lead to a stasis of blood in the organs of generation; the consequence of this must be to cause a kind of erection in the vessels the structure of which is similar to that of the *corpora cavernosa*, leading to a hæmorrhage within the uterus, but in the ovary to an increase in the contents of a follicle due to the transudation, and ultimately to the bursting of the follicle.

The further changes which the liberated ova undergo will be discussed farther on, when the results brought about by impregnation are considered.

Formation of Semen.

Human semen in the condition in which it is evacuated is a very tough, white, alkaline fluid, possessed of peculiar odour, and assuming a more fluid consistence when exposed to air. It is a mixture of the secretions of the glands which empty themselves in the excretory passages, with the original secretion from the testicles; the latter is alkaline or neutral, is destitute of smell, and dries more readily.

The semen contains a large number of seminal corpuscles, about 0.05^{mm} long, the body of which is almond-shaped and terminates in a tapering tail. The movements of the spermatozooids are pendulum-like or wave-like vibrations of the tail, by which the body is driven forward in a straight line, at a rate varying between 0.05^{mm} and 0.15^{mm} in the second, until, meeting with an obstacle, its direction is altered. The movement of spermatozoa is most rapid in semen which has just been evacuated; it is slow or absent in semen from the testicle. The duration of the movement depends upon a variety of circumstances, which, in general, are the same as those which influence the ciliary motion.

The motion of spermatozooids continues longest in fluids the concentration of which is the same, or very nearly the same, as that of semen, and is especially active in the secretion of the seminal passages (as in the prostatic secretion, Cowper's secretion, &c.), as well as in that of the female genital organs. The motion very soon ceases in very dilute fluids, in water and in saliva. Quite independently of the state of concentration, the following substances arrest the secretion: many metallic salts, mineral acids, alcoholic and ethereal substances, &c. On the contrary, the caustic alkalies under certain circumstances restore the arrested movements of spermatozoa. The cause of these movements is quite unknown; some consider the head to be the active organ of movement (Grohe), and others the tail (Schweigger-Seidel, v. La Valette St. George); the relations between the movements of spermatozoa and those of protoplasm and of cilia have already been spoken of in Chapter VIII.

The principal chemical constituents of the semen are: albuminous bodies, protagon, fats, water, and salts (potassium salts, phosphates).

The formation of semen takes place in the testicle, the cells of the 'seminal tubes' furnishing the spermatozoa. The statements relating to the formation of the latter in man are not yet certain. Most probably several or many spermatozoa originate in one cell, from nucleated oval vesicles, of which each one develops at one end the tail of a spermatozoon; ultimately the parent cell falls to pieces, setting free the spermatozoa; occasionally fragments of the cell remain connected with the spermatozoa and admit of being recognised (Kölliker). According to other observers the semen-forming cells possess but one nucleus, and the nucleus grows as the head of the spermatozoid out of one side of the cell, whilst opposite to it the protoplasm of the cell grows out as the tail of the spermatozoid (v. La Valette St. George). The semen-forming cells originate by division from the glandular cells, which lie in the axis of the tubuli seminiferi (lately different statements have been made on this matter, which are, however, doubtful). The fluid part of the semen originates by unknown secretory processes in the tubuli seminiferi; in all probability the specific constituents of the fluid proceed from the same cells which furnish the spermatozoa. The spermatozoa of the tubuli seminiferi exhibit either no movements or only slight ones. The formation of semen appears to proceed continuously. Nothing is known in reference to the nerves which preside over this secretion.

The semen, when formed, after it has passed through the spongy cavities of the 'corpus Highmori' and the canals of the *epididymis*, is carried by the *vas deferens* into the *vesiculæ seminales*, where it accumulates. On its way it mixes with the secretion of the mucous membrane of the *vas deferens*, the inferior extremity of which presents racemose glands, as well as with the secretion of the *vesiculæ seminales*.

The emission of semen takes place by reflex action through irritation of the penis, during sexual intercourse, during sleep under the influence of weak irritations associated with voluptuous dreams (seminal emissions caused by pressure of urine).

Under normal circumstances, erection of the penis must precede emission of semen, *i.e.* the three corpora cavernosa become filled with blood, so that the penis becomes lengthened and stiffened, and assumes a rounded prismatic form; at the same time it becomes erect, and slightly concave on its dorsal surface. The nature of erection has not yet been sufficiently made out.

The corpora cavernosa constitute a communicating system of cavities, in which open the finest twigs of the arteries which run in the septa, and from which the veins proceed. As the septa contain smooth muscular fibres, and can therefore actively alter the lumen of the corpora cavernosa, two explanations of erection are possible, *viz.*: 1. The flow of blood out of the corpora cavernosa may be hindered by compression of the efferent veins. 2. An increased flow of blood into the corpora cavernosa may occur by the cessation of a tonic contraction which is present during rest (Kölliker).

Both phenomena appear actually to occur, as the following experiments prove: 1. Diminution of a tonic contraction of blood-vessels; in the dog irritation of the *nervi erigentes* (fibres which proceed from the sciatic to the hypogastric plexus) causes erection (Eckhard). During this irritation any arteries of the penis which may have been cut across bleed more freely (Lovén); erection can therefore not merely be due to a hindered efflux of blood, but it must depend upon the abolition of a contraction of vessels, the mechanism of which is not known; the pressure of blood in the vessels of the penis, even during the strongest erection, only amounts to one-sixth of the pressure in the carotid artery (Lovén). The action of the nerves which influence erection may be placed side by side with that which the fibres of the *chorda tympani* exert on the salivary glands.

The vaso-motor nerves of the penis are contained in the *pudendal nerve* and in the *nervi dorsales penis*; a section of these alone does not cause erection; it however prevents erection in the future (Hausmann and Günther).

2. A compression of the efferent veins appears to occur, especially when erection is at its height; this is effected (*a*) by the

m. transversus perinæi, through which the venæ profundæ pass (Henle); (b) by trabecular projections, composed of smooth muscular fibres, into the veins which compose the plexus Santorini (Langer); (c) by the venæ profundæ themselves passing through the corpora cavernosa (Langer). The immediate centre which presides over erection appears to exist in the lumbar portion of the spinal cord (Goltz). After cutting across the cord between the cervical and dorsal regions, mechanical irritation of the penis of dogs still leads to reflex erection (strong irritation of sensory nerves prevents this, as it does other reflex actions), though not after destruction of the lumbar portion of the cord. The brain is in connection with this centre, as results from the fact that erection of the penis is brought about by psychical conditions, further that it follows irritation of the crura cerebri, of the cervical portion of the cord (Ségalas, Budge, Eckhard). Erection often occurs in persons who die by hanging.

The arteries which lead to the corpora cavernosa ('helicine arteries') follow a very curved course, so that a great increase in the volume of the penis may occur without any dragging of the arteries.

Sexual Intercourse.

Whenever the sexual passion is excited, erection sets in, and it precedes the emission of semen. The latter phenomenon only occurs after mechanical irritation of the penis, as occurs during sexual intercourse by its friction against the rugose walls of the vagina. It therefore occurs as a reflex movement.

The emission of semen from the vesiculæ seminales into the urethra probably occurs by peristaltic contraction of the vas deferens and vesiculæ seminales, whilst the emission from the urethra is the result of rhythmical contractions of the bulbo- and ischio-cavernous muscles. The passage to the bladder is shut off by the erection of the 'caput gallinaginis,' which at the same time prevents the passage of urine during erection. The secretions from the prostate and from Cowper's glands mingle with the semen which is excreted. Even in the genital organs of woman, as a result of the sensory irritation which takes place during coitus, certain reflex movements occur, which probably further the passage of semen into the most internal organs. Amongst such movements have been surmised the assumption of a more perpendicular position of the uterus, which is perhaps due to an erection of this organ (Rouget), and, probably, peristaltic movements of the uterus and Fallopian tubes, taking place in the direction of the ovaries (such movements have at any rate been observed to occur in the lower animals). Such movements would explain how a portion of the semen is conducted to the ovary, in spite of the movements of

the ciliated epithelium, which are opposed to its passage, as the irregular movements of the spermatozoa could not be utilised in effecting the passage upwards. After emission of semen erection very soon ceases, as well as the psychical and physical excitement which accompanies it; the latter disappears more rapidly in man than in woman. In both sexes there ensues an exhaustion, which continues for some time.

Impregnation.

The seat of contact between ovum and semen has not yet been determined with certainty, but in all probability it occurs generally in the ovary itself, or in the vicinity of the Fallopian tubes, seeing that in mammalia, after intercourse has taken place, the surface of the ovaries is generally covered with spermatozoids (Bischoff); in this way is to be explained the occasional occurrence of ovarian and abdominal pregnancies. Closely connected with this question is the one as to whether, with sexual intercourse, there is associated a liberation of ova similar to that which occurs during menstruation, or whether, in fertile coitus, only the ova which are liberated before or after menstruation are impregnated. In favour of the latter view is the analogy with mammalian animals which can only be impregnated during the 'period of heat.' As the human female can be impregnated at any time, we must, if intercourse cannot effect a liberation of ova, suppose that either the still present ovum of the last menstruation remains capable of fertilisation, and is actually impregnated, or that the semen remains in the female generative organs, perhaps even in contact with the ovary, until the next ovum is liberated, and is still able to fertilise it. Probably both processes occur. Concerning the process of impregnation and the first stages of development, there exist, in the case of man, no direct observations. We are therefore here compelled to reason by analogy from the other mammalia, as must necessarily be done in the exposition which is to follow of the processes of development. The youngest fecundated ova obtained as a result of miscarriage, or of the death of the mother, exhibit only tolerably advanced stages of development.

The impregnated egg is most probably impelled by the ciliary motion of the mucous membrane of the Fallopian tube into the uterus, to the mucous membrane of which it attaches itself, and in which it is usually found embedded. Presumably the process proceeds in such a manner that the surrounding parts of the mucous membrane increase in size, and grow over the ovum, the portion which has grown over, which is called the 'decidua reflexa,' increasing in size with the ovum.

According to another view the ovum places itself behind the

uterine mucous membrane (*decidua vera*), and thrusts it before itself; according to Funke, the process consists in the ovum sinking into a uterine gland, as is really the case in the guinea-pig, and perforating its base.

At a later stage of development, after the embryonal vessels have been formed, an intimate interlacement with those of the mother takes place (*placenta*). The excessive development of a *corpus luteum (verum)* during pregnancy points to the periodic liberation of ova being interrupted by it. The interruption usually continues during lactation, as is evidenced by the fact that menstruation usually is absent, and especially because fresh *corpora lutea* are usually not formed in suckling women.

An incipient formation of a *decidua* appears to occur with each liberation of an ovum, the uterine mucous membrane being swollen; and this appears to be the cause of the menstrual hæmorrhage (*Pflüger*).

C. DEVELOPMENT OF THE OVUM IN THE MAMMALIA AND MAN.

Segmentation.

The first process in the development of the ovum is that of *segmentation*.

It begins in *mammalia* as early as a few hours after the contact of the semen with the ovum, or after the entrance of the spermatozooids into the yolk (perhaps even earlier), so that the ovum only reaches the uterus at a tolerably late stage of development. Segmentation consists in a progressive cell-division, by which each spherical cell splits up into two half-spheres. Whether the first cell is identical with the 'germ-cell' (with the principal yolk), or whether it first originates by transformations of that cell, is doubtful, and the same remark applies to the germinal vesicle, which is invisible before segmentation, as well as to the manner of cell-division and the division of the nucleus.

Segmentation proceeds very rapidly (its duration in man is unknown; in the rabbit it lasts some days, and in the dog more than eight days) and furnishes in the end a large number of small, spherical, strongly refracting cells, which together present a mulberry-like appearance.

During segmentation the ovum, whilst in the Fallopian tube, loses the *discus proligerus*, and either surrounds itself, as the rabbit's ovum, with accessory envelopes, or the *zona pellucida* first receives in the uterus (as in the human subject) the first envelope of fine radially arranged villi, which ramify and form a thick villous covering around the ovum; the *zona* then receives the name of *chorion* (*frondosum*).

Rudiment of the Embryo.

The disposal of the cells which have been produced in the process of segmentation for the purpose of building up the embryo commences with the deposition of their greater part on the inside of the zona pellucida, to form a closed membrane which is called the germ-vesicle (*'Umhüllungshaut,'* Reichert). At a certain part of the membrane a more considerable accumulation of cells takes place, destined directly for the formation of the embryo, and this is called 'the germinal area.' The cavity which results from the deposition of cells, as well as from the enlargement of the ovum, is filled with fluid, or in eggs which possess a food-yolk, contains the latter.

In order to understand the development of the embryo a somewhat different consideration of the fully developed animal body than that usually given by descriptive anatomists is requisite. Let us conceive a mammal with a short straight alimentary canal, and let us lose sight of all glandular organs; the body may then be considered as a tube, the lumen of which is the lumen of the alimentary canal and the wall of which is composed of many concentric layers, viz. (from within outwards): intestinal mucous membrane, muscular coat of intestine, serous coat of intestine, parietal layer of peritoneum, muscular layer of trunk, osseous layer of trunk, skin covering trunk. All these layers grow together; only between the visceral and parietal layers of the peritoneum, up to the mesentery situated in the middle line behind, there is no fusion, but a cavity, the pleuro-peritoneal cavity, which is, however, empty, so that its walls are always completely in contact with one another. The ideal tube which we are imagining possesses complete symmetry. Its extremities, which have no openings, may be looked upon as bulky outgrowths from the external wall of the tube.

The embryonic development of the tube takes place in general in the following manner: the wall arises in the commencement as a flat thickening of the first-formed *germ vesicle* which everywhere surrounds the ovum; this thickened spot splits up by degrees into the different layers which correspond to the strata in the wall of the ideal tube.

The cavity, however (the intestinal cavity), is a part of the germ-vesicle, which separates from the rest by the thickened portion of the vesicle—that which is to form the wall of the embryo—partly shutting itself off from the rest of the vesicle, in the form of a lengthened tube. The main portion of the germ-vesicle (which is not included within the embryo) is then called the

umbilical vesicle, and the canal-shaped communication which by the ever increasing constriction becomes progressively narrower, and establishes a communication between the cavity in the embryo (intestinal cavity) and that of the umbilical vesicle, is called *the umbilical duct* or ‘ductus vitello-intestinalis seu omphalo-entericus.’ The ultimately ring-shaped place of constriction is *the navel*; as the thickening and even the division into layers of the germ-vesicle does not limit itself to the portion which becomes constricted, but extends beyond the point of constriction towards the peripheral parts of the vesicle, it follows that even the wall of the navel consists of several embryonic layers.

The formation of layers over the germinal area of the germ-vesicle, which, in great part, begins even before the commencement of the shutting off of the embryonic cavity, is variously described. Only one view, which in the main is Remak’s, will here be given; the others will be, however, cursorily examined.

Three layers—the three layers of the blastoderm—form in the smooth at first oval, then hour-glass-shaped thickening of the germ-vesicle. The most external or uppermost—‘the *epiblast*,’ the sensory layer—is the seat of the cutaneous epithelium with its appendages, the glands of the skin, and of the central organs of the nervous system (brain and spinal cord) with its appendages, the organs of the senses.

The central nervous system originates in the central (axial) part of this layer in the so-called *medullary folds*; the epithelium of the skin is formed from the peripheral part or ‘*corneal layer*’ of the epiblast.

The innermost of the three layers of the blastoderm—‘the *hypoblast*’—is the seat of the intestinal epithelium with its appendages, viz. the epithelium and the glandular cells of the glands which open into the intestine. Between the epiblast and the hypoblast lies the *mesoblast*, the motor and germinative layer from which all the rest—all the parts of the body which consist of connective tissue, muscles, vessels, and nerves, as well as the urinary and generative organs—are formed. This layer splits up very early into two plates; the external forms the wall of the trunk, the internal forms the wall of the intestine, with the exception of the epithelium; the space between these secondary layers constitutes the already mentioned ‘*pleuro-peritoneal cavity*.’ Inasmuch as the division into these two layers is arrested in the middle line, there is here established a fusion between the wall of the trunk and of the intestine, and this is the seat of the mesentery (compare below, fig. 70, II., III., IV.)

Processes of Development in the Germinal Area.

In each of the three layers of the blastoderm there follow, in addition to the already mentioned process of constriction, certain processes of development by which they undergo transformation.

The chief of these processes are: 1. In the *epiblast* the *laminae dorsales* or *medullary folds* separate from the corneal layer and form a tube. 2. In the *mesoblast* the first commencement of a skeleton takes place; further, the division already alluded to and the formation of a vascular system commences. 3. From the *epiblast* and *hypoblast* processes of epithelium grow into the tissues from out of the middle layer, so that there are formed hollow processes which are in part enclosed in the body cavity, and form glands.

Epiblast.

1. The first process to be mentioned is the one which first occurs. In the centre of the medullary fold a longitudinal groove is formed, dividing it into two symmetrical halves, which curve towards one another, drawing over themselves the corneal plates which are attached to them. The cause of this is the growing forwards of the processes of the middle layer, which tend to press themselves between the medullary plates, which are curved towards one another, and the corneal plate. Ultimately the medullary folds are closed, so as to form the medullary tube, and the corneal plates still attached to the point of union are, finally, completely separated from it by the union of the two lateral appendages of the middle layer, in such a manner that the medullary tube is thenceforward entirely enveloped in a prolongation of that layer. This envelope forms the spinal arch, together with the muscles, the ligaments, and the skin of the back (which last receives a covering from the corneal layer, viz. the epidermis), and at the anterior extremity (head) the cranial capsule.

The medullary tube becomes the spinal cord and brain; its interior is converted into the central canal of the cord, with its connection in the brain—the so-called ventricles of the brain (compare below, fig. 70, II., III., IV.)

Mesoblast.

2. The simultaneous phenomena of development which take place in the *mesoblast* concern the vertebral system.

The centre of this system is a streak which is very early

developed, and which runs in the median plane of the embryo, and which is called the 'chorda dorsalis.' On each side of this there appear two longitudinal plates, the *protovertebral plates*, which by transverse lines subdivide themselves into a number of *protovertebræ*. The remainder of the mesoblast, so far as it belongs to the germinal area, forms 'the lateral plates.' The *protovertebræ* undergo the following changes: they develop 'spinal processes,' the influence of which upon the formation of the canal of the cerebro-spinal organs and upon the union between this and the separated corneal plates has already been mentioned. Internally the *protovertebræ* grow around the *chorda dorsalis* (see below, fig. 70, II., and following).

Their substance is converted into various tissues, viz. into the vertebral column with its appendages, into the ribs and the muscles pertaining to them, into the spinal nerves and the skin of the back. The bodies of the *vertebræ* originate in the part which surrounds the notochord in such a manner that in the middle section of each *protovertebra* there is formed an intervertebral cartilage, and from the fusion of adjacent halves of the *protovertebræ* a persistent vertebral body originates.

In the lateral plates there occurs further the already mentioned splitting up of the embryonal wall into the two layers; the internal attaches itself to the hypoblast, and forms with it the *splanchnopleure*, the external attaches itself to the epiblast, and forms with it the *somatopleure*. The separation between these two layers forms the *pleuro-peritoneal cavity*; the internal undivided edges of the *lateral plates*, advancing together little by little on the ventral side of the vertebral column, form the so-called *middle plates*, which are the foundation of the *mesentery*, and foetal urinary and generative organs. The former of these two sets of organs originate as a string-like thickening of the middle plates, which later on becomes hollow; according to some as an invagination of the *pleuro-peritoneal cavity*—the *Wolffian canal*. For the further development of this organ, and the other urino-generative organs, see below.

The third process which takes place in the mesoblast is the development of the *vascular system*.

This system first originates in that layer of the mesoblast which goes to form the *splanchnopleure*, and makes its way outwards in the yet undivided peripheral part of the mesoblast. The manner in which the vessels and the blood are formed has not been accurately determined, yet, according to the majority of statements, it occurs as follows: cellular trabeculæ are interwoven so as to form a network; the peripheral layers of cells are then converted into vascular parietes, and the contained cells become at first colourless nucleated blood-corpuscles. According to a new view (Klein) the vessels originate in cells which become hollow,

which lengthen out and run together, and from the nuclei of which the blood-corpuscles are formed.

The area over which blood-vessels are formed is considerable, occupying an important circularly-bordered portion of the germ-vesicle, which is called the *area vasculosa*.

Of all vessels the first formed is *the Heart*; it originates in the most anterior part of the splanchno-pleure which has already become closed into a tube.

The following may serve to explain the position of the heart: the amnion-fold is formed more rapidly at the head and tail than at the sides. At a certain stage of development the *embryonal wall* which is shutting itself off from the *germ vesicle* resembles a shoe somewhat *trodden down at heel* (see fig. 70, I.), the free borders of which pass into the main part of the germ-vesicle. The opening of the shoe represents the still widely open *navel*; the shoe cavity represents the interior of the intestine. Along the middle line of the sole of the shoe (which represents the dorsal surface of the embryo) the cerebro-spinal tube would be situated. The wall of the shoe is throughout double, up to a streak in the middle line of the sole (the mesentery); at the end of the shoe and on the uppermost part of the anterior layer (the shoe being supposed to be suspended vertically with the heel downwards, but with the opening towards the observer) the wall is also single, the body—and intestinal—wall being united. This unsplit upper part of the anterior wall is called the '*pharyngeal plate*.' From the cavity of the germ-vesicle one may pass through the navel into the anterior part of the cavity of the embryo, which has now already assumed the shape of a tube (this part, which is transformed into the *foregut*, is called the '*fovea cardiaca*'), as well as into the posterior, shallower, '*foveola posterior*.' That part of the wall of the '*fovea cardiaca*' which is directed towards the *germ-vesicle* (the anterior wall of the hypothetical shoe) is, below the '*pharyngeal plate*,' also double like the main part of the sole. Of the two layers the inner one represents the anterior wall of the foregut, and the external that portion of the pleuro-peritoneal cavity which lies in front of the intestine (refer to fig. 70, I., V., VIII.)

The heart originates in the median line anteriorly, according to some (Remak), as a cylindrical thickening of the anterior wall of the foregut (see fig. 70, V., VI.), which thickening soon becomes hollowed out, and appears to be in connection with the remaining vessels; according to others (Schenk, Oellacher), as a process of the wall of the foregut, which shuts itself off and grows forwards *into* the cavity lying in front of the intestine referred to in the preceding paragraph. The vessels which are connected with the heart are to be followed in two directions. The arterial vessels commence with two aortic arches starting from the anterior extremity of the heart, which curve inwards and backwards along the pharyngeal plate and which, separated at first throughout the length of the chorda dorsalis, later on unite to form the aorta, and terminate in the arteriæ iliacæ communes.

Instead of one there are generally several (three) aortic trunks on each side, which, however, again unite on each side to form an *aorta* or aortic root. On each side there springs from the aortæ a series of vertically ascending arteries, which run on the sides of

the splanchnopleure, and which go to the *area vasculosa*, where they ramify; these are called the *omphalo-meseraic* arteries. Two venous trunks pass into the posterior end of the heart through a short common trunk; these vessels also are distributed over the *area vasculosa* and are called the *omphalo-meseraic veins*.

Both the above sets of vessels communicate through a circular vessel which limits the *area vasculosa*, and which is termed the *sinus terminalis* (see fig. 70, I.) This system of vessels probably serves as a first respiratory apparatus, as well as to convey to the foetus the nourishment which is yielded by the contents of the germ-vesicle. It disappears early in proportion as the contents of the vesicle are of little importance in nutrition, and is at a later stage replaced by the allantois, which subserves the same functions. As soon as it is formed the heart begins to pulsate, so that the blood-corpuscles commence at once a somewhat irregular circulation through the newly-formed vessels.

Hypoblast.

From the inner layer, the development of which commences latest, processes are protruded which grow into that part of the mesoblast which is contained in the splanchnopleure,¹ and form the small glands of the alimentary canal, as well as the liver, the pancreas, and, in addition, the lungs and the permanent kidneys. It is easy to see how the protrusion of the hypoblast must form the epithelium, or the cells of a glandular canal, whilst the invaginated splanchnopleure must form the connective tissue, the blood-vessels, the nervous and the muscular surroundings (the basis of the gland). If the protrusion proceeds so far that even the splanchnopleure is protruded, as in all large glands, the protruded intestinal wall must evidently project into the pleuro-peritoneal cavity, as is the case in reality with all the glands which open into the intestine and which are surrounded by peritoneum.

The liver originates by the protrusion of two hollow processes (primitive hepatic ducts) from the foregut, close to the navel; the finest branches form the very complex network of hepatic canals which, with the blood-vessels, constitute the parenchyma of the hepatic lobules. The larger canals are the biliary ducts, and a projection from one of the primordial canals forms the gall-bladder. The liver grows around the trunk of the omphalo-meseraic vein, which communicates with its vessels. One of the intestinal veins which enter into it, and which is permanent, forms later on with those branches the *portal vein*.

Opposite to the liver, and starting from the posterior intestinal wall, there arises by ramifications, and afterwards hollowing out, an outgrowth which is at first solid—the *pancreas*.

¹ By this it is not intended to ascribe in any way an active part to the epithelium; it is indeed more probable that the in-growth of epithelium is conditioned by the growth of the splanchnopleure.

A further double projection from the anterior wall of the intestine, but above the heart, and which penetrates the pleuro-peritoneal cavity, forms *the lungs*, with their *bronchial system*, the entrance to the lungs being therefore situated in the foregut (later the pharynx). For the development of the kidneys see p. 549. Lastly, the thyroid and thymus glands have to be considered; the first arises as a vesicular outgrowth from the anterior wall of the foregut, which shuts itself off, then by further processes of development divides into two symmetrical cavities, which respectively give rise to secondary cavities. The thymus gland is formed in a similar manner. The spleen, lymphatic gland and follicles, and the suprarenal capsules, originate from the mesoblast.

Peripheral Processes of Development.

Side by side with all the processes of development which have been described as proceeding in the germinal area, there are other processes taking place in the peripheral part of the germ-vesicle, which have for their object to permit the embryo to develop freely on all sides by embedding it in a fluid (amnion), and also to bring the foetal blood into relations permitting of diffusion-changes taking place between it and the maternal blood, whereby nutrition and respiration are rendered possible (*'allantois'*).

1. Development of the Amnion.

It has already been mentioned that a cleavage of the germinal area into blastodermic layers proceeds beyond the embryonal area to the peripheral parts of the germ-vesicle, and that the same is true of the cleavage of the mesoblast. The latter cleavage, however, does not extend over the whole germ-vesicle, but only so far as the area vasculosa extends. Here the superficial layer ceases, so that at this spot, provided that the epiblast has been broken through, the space between the two layers of the mesoblast, and ultimately the pleuro-peritoneal cavity, may be reached. The peripheral parts of the external portion of the mesoblast (*'Hautplatte'*) now rise up from the germ-vesicle and arch backwards on all sides of the embryo, driving the epiblast before them, and coming from all sides join above the embryo, enclosing it in a sac which is called the amnion; the layer of the epiblast which is enclosed lines the inner surface of the amniotic sac.

The amnion is filled with a serous fluid, by which the embryo is surrounded on all sides; besides the normal constituents of transudations, it contains secretions from the skin and nitrogenous products of oxidation, presumably as a result of diffusion from the allantois.

2. Formation of the Allantois.

Near to the caudal end of the embryo in the region of the navel there originate two solid accumulations of cells, which grow

from the external layer of the mesoblast, and which soon unite. Into this out-growth, which lies close to the splanchnopleure, there grows a process of the posterior part of the intestine in such a manner that a vesicular cavity is formed; this bladder, *the allantois*, grows out of the embryo between the somatopleure and the splanchnopleure, reaching the space between the amnion and the germ-vesicle; growing always more and more extensive, it envelops the amnion and reaches the inner wall of the *chorion*, with which it becomes connected over a greater or smaller surface. The communication between the posterior part of the intestine and the allantois forms the *cloaca*, into which empty themselves the foetal urinary organs. The part of the allantois which becomes small, and which passes through the umbilical orifice, is called *the urachus*. The allantois is highly vascular. The arteries, the *umbilical arteries* spring from the common iliacs; they lead to a well-developed capillary system, the loops of which enter the chorionic villi; the veins unite to form the single *umbilical vein*, which, returning to the embryo, opens into the omphalo-meseraic vein, and thus communicates (as the *portal vein*) with the blood-vessels of the liver; it sends a branch directly to the *vena cava inferior* (*ductus venosus*).

The well-developed *villi of the chorion*, which contain the blood-vessels of the allantois, grow into the interior of the uterine mucous membrane, in which, at the corresponding spot, corresponding capillary loops are formed. The two sets of vessels together form the placenta, in which an exchange by diffusion proceeds between foetal and maternal blood, for the purposes of respiration and nutrition; the blood of the umbilical vein is therefore necessarily brighter (more arterial) than that of the corresponding arteries, exactly as at a later period of existence the blood of the pulmonary arteries and veins differ. The umbilical vesicle and the area vasculosa now lose their importance, and, together with their blood-vessels and the umbilical duct, shrivel together so as to form a thin string. The fluid which the allantois contains is a transudation containing the secretion of the primordial kidneys, with some nitrogenous products of oxidation.

While in man only one placenta is developed, animals possess several placental sites, so that the villi of the *chorion* enter the villi of the decidua in many places.

Final Stages of Development of the Embryo.

If we imagine the body cavity of the embryo to have been shut off from the germ-vesicle, the umbilicus will consist of two concentric tubes; the inner (the omphalo-meseraic duct) connects the intestine with the umbilical vesicle; the outer is formed by skin, and connects the abdominal wall of the embryo with the amnion.

Between these concentric tubes there exists a circular space, through which the pleuro-peritoneal cavity may be reached, and through which the urachus comes.

By a simple process of separation by constriction, an intestinal tube, closed on all sides, is formed, which is united in the median line posteriorly to the body cavity (by the mesentery), and to the whole upper end of the body. Subsequently there are formed an anterior and a posterior intestinal opening. In the anterior part of the centre of the pharyngeal plate, close below the fore-brain, there is formed a depression into which the epiblast passes. This depression becomes deeper and deeper, and ultimately opens by a fissure into the upper end of the fore-gut (pharynx), forming the buccal and nasal cavities.

Further, there are formed on the lateral parts of the pharyngeal plate three gutter-shaped cavities of the hypoblast, which run from before backwards; these ultimately break through the pharyngeal plate, and form on each side three *visceral* or *branchial clefts*, and later on yet a fourth, by the hypoblast making a border, as the mucous membrane gives an external mucous edge to the lips; between each pair of pharyngeal plates there remains a *pharyngeal* or *branchial arch*, which is so arranged that on its inner side an aortic arch runs from before backwards. Along the pharyngeal arches thickenings arise from before backwards, and ultimately meet. The space between the skull and the first pharyngeal arch is taken up by the buccal and nasal cavities; the first pair of branchial arches is converted into a lower jaw and the neighbouring parts of the cranium; as, however, it sends two branches into the common buccal and nasal cavity, which grow so as to meet, and which develop into the upper jaw and gums, a separation between the buccal and nasal cavities is ultimately effected. (It is from an arrest in the development of these processes that hare lip and cleft palate result.)

The remaining visceral clefts unite, the branchial arches furnishing the hyoid bone, a portion of the laryngeal cartilages, the skin of the neck, &c., by processes which cannot here be examined in detail. The tongue originates as an outgrowth from the inner side of the lower jaw. The posterior intestinal opening originates in a perforation of the *cloaca*, which is the common termination of the intestine and the allantois.

This common aperture is afterwards subdivided by a bridge, the *perinæum* (which is an outgrowth of the wall which separates the intestine from the allantois), into one connected with the bowel, viz. the *anus*, and into one communicating with the allantois (opening of the *uro-genital sinus*).

The first pair of visceral clefts unite, except where an opening is left, which is the rudiment of the external auditory meatus. The second, third, and fourth clefts unite completely; as the

aortic arches bend back from the inner side of the branchial arches, and take with them the mesoblast, the third and fourth clefts grow deeper.

Of the remaining processes of development the following must be mentioned :

1. The 'medullary or neural tube,' the cavity of which continually diminishes by an increase of the thickness of its walls, very early shows, at its dilated cerebral end, two transverse depressions which mark off three *cerebral vesicles*. Each vesicle carries on either side a vesicular outgrowth, which subsequently becomes pedunculated, which represents the rudiments of the three higher organs of special sense with their respective nerves—the first is the olfactory, the second the optic, and the third the auditory; the vesicles are the rudiments of the peripheral nerve distribution. In the optic vesicle, which is immediately beneath the corneal layer, a vesicular involution of the latter takes place, which ultimately becomes shut off and forms *the lens* with its *capsule*. The optic vesicle thus invaginated in itself becomes converted into an hemispherical body by the anterior half (the *retina*) being placed in close apposition with the posterior (the *choroid*). Between the lens and the retina there then originates the *vitreous-body*, and around, by a process from the mesoblast, the *sclerotic*, which unites with the portion of the skin which covers the eye so as to form the cornea.

The three cerebral vesicles represent, from before backwards, the *third ventricle*, the *aqueductus Silvii*, and the *fourth ventricle*. The first gives off a new vesicle on each side, the interior of which represents the *lateral ventricles* (the communication between these and the primitive vesicle is formed by the *foramen of Munro*), and their walls represent the cerebral hemispheres; the lateral vesicles in man outgrow all the others.

In a similar manner the third cerebral vesicle sends out two *cerebellar* vesicles. Between the first and the second vesicle there arises early a tolerably sharp constriction, so that the former bends around the anterior extremity of the embryo.

The cerebral ganglia (optic thalami, &c.) arise as a thickening of the vesicular walls.

Statements vary as to the origin of peripheral nerves and ganglion-cells. The majority of authorities believe them to originate in the mesoblast; others (Hensen) believe the axis cylinders to arise as outgrowths from the ganglionic cells of the central nervous system into the mesoblast, which furnishes, however, the sheath and white substance of Schwann.

2. The intestinal canal forms at first a simple tube, which is only slightly bent in the centre, where the mesentery is longest.

In the vicinity of the liver a dilatation of this tube occurs, marking the position of *the stomach*, which subsequently, by a movement of rotation, takes up its persistent transverse position

and thus presents a *fundus* and two *curvatures*. By an elongation of the intestinal tube, and a simultaneous elongation of the mesentery, are formed the coils of the small intestine and the curves of the large intestine. That piece of the omphalomesenteric duct which lies within the embryo, breaks at the navel and forms a rudimentary appendage of the lower part of the ilium.

3. The heart, which in the beginning is a straight tube situated in the middle line, very early alters its form, so that its venous (posterior and inferior) end bends itself towards its arterial end, so that the whole organ, with the origin of the veins, takes the form of an S (see below, fig. 70, I.) The cause of this is that during a certain time the aortic arches increase in number posteriorly, whilst those situated anteriorly disappear; hence the anterior part of the heart is thrust backwards, whilst the venous end retains its original position. Three parts of the heart, which contract one after the other, may now be recognised, viz. *sinus venosus* (from which the two auricles afterwards spring), *ventricle*, and *bulbus aortæ*. A longitudinal partition wall is now formed, at first in the ventricle and afterwards in the auricle (being incomplete here), whereby two separate ventricles are formed, and two auricles communicating through the *foramen ovale*. Of the three remaining pairs of aortic roots, the first forms the carotid and subclavian (on the right side the common trunk persists); the second forms on the left side the permanent aortic arch, which leads to the primitive descending aorta, and from which the vessels of the first pair spring; the right branch disappears.

The third pair furnishes the pulmonary arteries; the right arch disappears, except its pulmonary branch, and the left remains connected with the descending aorta, the connecting piece forming the *ductus arteriosus* (duct of Botall). Ultimately the bulbus arteriosus divides itself in such a manner that the section which gives off the pulmonary arteries remains connected with the right ventricle, whilst the remainder, with the arch of the aorta, remains attached to the left ventricle. Even then all the blood can pass from the right heart into the aorta, partly through the *foramen ovale*, and partly through the *ductus arteriosus*. It is only after birth, when respiration through the lungs has commenced, that both these communications are closed, and thenceforward the whole of the blood of the right heart is carried to the lungs.

4. *The internal urinary organs* are developed in the following manner: the structure in which they originate, the *Wolffian duct*, is at its upper end closed, and communicates below with the posterior part of the intestine (*foveola posterior*). The anterior end of the duct sends inwards a row of little blind canals, which are in part furnished with *glomeruli* (derived from the mesoblast). Thus arises the *Wolffian body*, of which one part, the primordial

kidney, discharges the functions of a kidney, whilst the remainder (the sexual part) goes to form the organs of generation.

The *permanent kidneys* are formed (Kupffer) by a tubular protrusion from the tail-end of the Wolffian duct; this protrusion pursues a course parallel to that of the primordial kidneys, and grows upwards as the rudiment of the *ureters*; the upper end grows into a mass of cells derived from the mesoblast (parenchyma of the kidney), and thus originate the *pelvis of the kidney* and the *calyces*. The *tubuli uriniferi* are either (Remak) further outgrowths from the calyces, the dilated ends of which (*capsules*) surround the glomeruli, or (Kupffer) they originate independently in the kidneys (from the periphery outwards), and only afterwards open into the calyces. (For the development of the urinary bladder, the reader must refer to the paragraph relating to the external organs of generation.)

5. The *internal organs of generation* are originally hermaphroditically disposed in both sexes. The peritoneal squamous epithelium which invests the free surface of the Wolffian duct is sharply separated from a layer of cylindrical epithelium which is placed upon the middle and the lateral angles; this epithelium (*germinal epithelium*), which probably is derived from the epiblast, is the rudiment of the female generative apparatus, viz., in the middle of the ova and the cells of the m. granulosa, and laterally of the epithelium which lines the Fallopian tubes and the uterus. The union of the median part with the connective tissue of the Wolffian bodies which leads to the formation of the ovary, has already been spoken of. The lateral layer of epithelium is similarly surrounded by connective tissue and presents the appearance of a longitudinal cord, which later becomes hollow and gives rise to *Müller's duct*, which occupies the position of the future Fallopian tubes.

The two Müller's ducts open not far from the Wolffian ducts into the hindgut. Later on, their lower ends unite to form a common chamber, the uterus and vagina. Above, in the vicinity of the ovary, an opening forms in the ducts, and this opening is surrounded by fringes. The piece of the duct above the opening becomes reduced to the condition of a vesicle. In the male embryo the testicle arises from the genital part of the Wolffian bodies, the canals of which, becoming very much elongated and arranged in coils, are converted into the *tubuli seminiferi*, which penetrate the connective tissue of the testicle; that portion which has not penetrated forms the *epididymis*, and the ducts of the primordial kidneys form the *vas deferens*, with the *vesiculæ seminales*. The tubuli which do not form a part of the testicle are the *vasa aberrantia* of Haller. In the female the genital part of the Wolffian bodies remains as *Rosenmüller's organ*, or the *par-ovarium*, the efferent passage being converted into the round

ligament of the uterus. In both sexes the renal part of the Wolffian bodies becomes reduced to the condition in which it is known as *the organ of Giralde*s or the *parepididymis*, and in the female as a separate structure situated close to the *par-ovarium*.

In the male, further, the seat of the ovary persists as a non-pedunculated cyst (Fleischl), whilst the ducts of Müller terminate below in the *uterus masculinus* (E. H. Weber) or *vesicula prostatica*, their upper end being represented by pedunculated cysts.

6. *The external urinary and sexual organs.* When with the closure of the navel the urachus is shut off, the portion of the allantois which remains in the embryo forms the urinary bladder (the vertex of which remains connected with the navel by the urachus). The lowest part of the allantois, which contains the openings both of the urinary and the sexual organs, is called the *sinus urogenitalis*. On each side of the opening of the latter there arise two cutaneous projections, which in woman give rise to the *labia majora*, but which in man grow together above the opening, to form the scrotum, closing by a persistent seam which is called the *raphe*. In front of the opening, further, there arises an elongated body, which bears on its lower surface a furrow, which posteriorly runs into the *sinus urogenitalis*. The edges of this furrow unite in man to form the canal-shaped *urethra*, which opens at the apex of the elongated body, the penis; the posterior part of the urethra is formed by the urogenital sinus itself. In woman, however, the furrow remains open, and its edges grow into the *labia minora* or *nymphæ*, whilst the original body itself forms the *clitoris*. The urogenital sinus becomes, however, so short that it merely forms a depression between the labia, into which the vagina and the urinary bladder with a short urethra separately open. In the male embryo the descent of the testes takes place into the scrotum at the eighth month; on this matter anatomical text-books are to be consulted.

Nothing is known in reference to the circumstances which influence the sex of the embryo. By statistics some have pretended to show that the relative ages of the parents have a certain influence in leading to a preponderance of males or females, still even this influence has been differently stated by different writers. Lately it has been asserted (Thury) that the sex depends upon the stage of maturity which the ovum has attained before impregnation; according to this view ova are at first only capable of developing embryos of the female sex, and only after having undergone a change are they capable of producing males. But this is by no means generally proved.

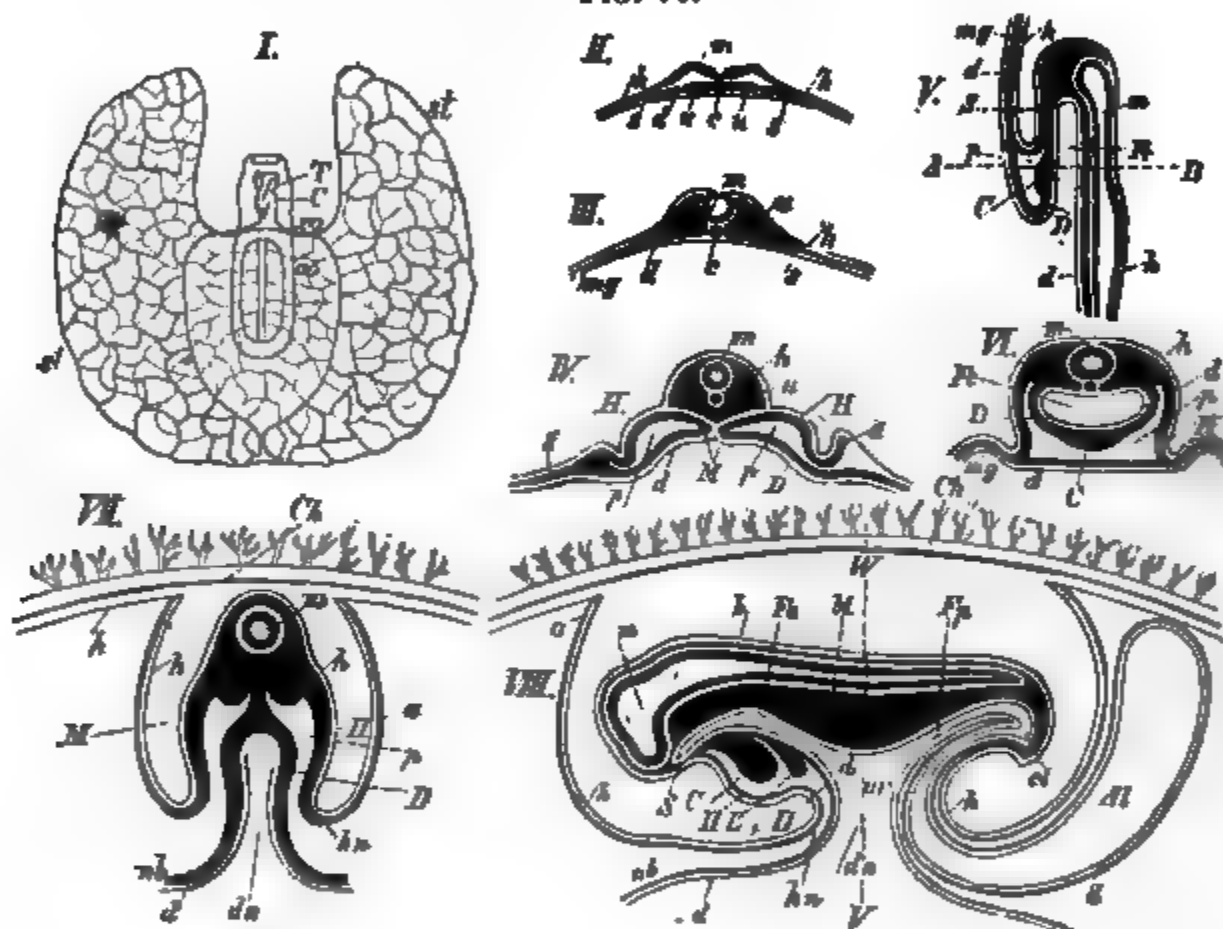
7. The extremities originate as warty processes from the sides of the trunk, which only subsequently increase in length.

The development of the tissues, which is one of the most important sections in the history of development, is usually treated of as a part of Histology, and the reader is therefore referred, on

this subject, to the works which specially treat of that branch of Anatomy.

The older theories of Pander, v. Baer, and Bischoff assumed principally the existence of only two layers of the blastoderm—an external or 'animal,' corresponding to the somatopleure, and an internal 'vegetative,' corresponding to the splanchnopleure; between these two that vascular system was supposed to originate from a separate vascular layer. A similar theory has lately been advanced by His, according to which, however, the whole system of connective tissues, the vessels, and the blood, are derived from the so-called 'white-yolk' (of the bird's egg), which has quite a different origin from the 'principal yolk' (archiblast, neuroblast). It (i.e. the white yolk) originates in the cells of the m. granuloza which have migrated through the vitelline membrane into the

FIG. 70.



principal yolk. The elements of the white yolk serve either for building up the embryo ('parablast,' 'haemoblast') by migrating between the two layers of the blastoderm, or merely as 'food-yolk.' Another theory (Reichert's) accepts the process of splitting up of the mesoblast ('stratum intermedium'), but differs from Remak's theory in not distinguishing a sensory (corneal) layer, and maintains that the original blastoderm persists as an enveloping membrane ('Umhüllungshaut'), whilst the proper layers are deposited within it afterwards. Between the enveloping membrane and the stratum intermedium originates the medullary plate as a special 'upper' layer, limited to the germinal area. That portion of the enveloping membrane which becomes shut off in the amnion forms the epidermis of the skin of the embryo, and furnishes an epithelial covering to the inner surface of the amnion ('endamnion'). Other recent modifications of the theory of Remak adopted in the text could not be here referred to without entering in a more special manner into the study of embryology.

The appended diagrammatic representations may serve to explain some of the fundamental points in development. With the exception of I., they are transverse sections of the embryo.

1. is a superficial view seen from the interior of the germ-vesicle; it shows the shoe-shaped embryo with the vessels of the area vasculosa. Across the anterior layer of the shoe, the already S-shaped heart is seen, from which superiorly there proceed two aortic roots, inferiorly, the two omphalo-meseraic veins. Through the opening of the shoe (the navel) the two still separated aortæ are seen, with the omphalo-meseraic arteries; in the area vasculosa the arteries are feebly, the veins strongly delineated.

The remaining figures are in part cross-sections (II., III., IV., VI., VII.), partly longitudinal sections of the embryo (V. and VIII.)

Section VI. corresponds to the line AB in the longitudinal section V.; the transverse section VII. corresponds similarly to the line VW in VIII. The letters of reference are the same in all the drawings.

h	Epiblast	hn	Cutaneous navel
m	Medullary or neural tube	Fc	Fovea cardiaca (foregut)
mg	Mesoblast	Fp	Fovea posterior (hindgut)
d	Hypoblast	a	Amnion (peripheral part of the external part of the mesoblast detached and inverted; in Fig. IV. on the left, it is yet connected with the internal part of the mesoblast; on the right it is detached)
e	Chorda dorsalis		
u	Protovertebral plates	Al	Allantois
s	Lateral plates	ur	Urachus
p	Pleuroperitoneal cavity	cl	Cloaca
H	External part of mesoblast	vo	Omphalo-meseraic veins
D	Internal part of mesoblast	ao	Omphalo-meseraic arteries
M	Mesentery	st	Sinus terminalis
S	Pharyngeal plate	L	Liver
Ch	Chorion frondosum		
nb	Umbilical vesicle		
C	Heart		
T	Aortic arches		
dn	Omphalo-meseraic duct		

So as to make the diagrams as intelligible as possible, in IV. and VII., the sections of the two aortæ and of the two Wolffian bodies are not shown.

Birth.

By the development of the ovum the uterus is more and more stretched, so that at the same time the cervix becomes obliterated. The uterine walls increase in thickness by the growth and by the new formation of its muscular fibres, as well as by the considerable development of its blood-vessels. At last, about 280 days after impregnation, by the operation of causes which are entirely unknown to us, the expulsion of the now-developed ovum takes place. This expulsion is brought about by rhythmical and painful contractions of the muscular fibres of the uterus, which are technically known as 'pains,' and which are aided by the compression of the abdomen.

The following facts are known in reference to the innervation of the uterus :

Irritation of the hypogastric plexus gives rise to uterine contractions, and the same result is obtained by exciting the spinal cord up to the cerebellum ; the fibres which pass from the spinal cord to the uterus leave it in the vicinity of the last thoracic, and the third and fourth lumbar vertebræ. They pass along sympathetic paths, traverse the inferior mesenteric ganglion and run in one of the nerves which lie over the aorta, until they reach the uterus (Frankenhauser).

In addition to the nervous supply derived from the spinal cord, the uterus appears to possess nerve centres in its more immediate vicinity, perhaps scattered in part through its parenchyma. These centres are excited by the blood of dyspnoea (Oser and Schlesinger), like the centres in the medulla oblongata and in the intestines, so that suffocation, compression of the aorta (Spiegelberg), hæmorrhage, &c., bring about uterine contractions. Even the centre presiding over uterine contractions, which is seated in the brain, is excited by the blood during dyspnoea, as well as by the circumstances previously mentioned (Oser and Schlesinger).

In the human being the ovum is not thrown off uninjured, but the embryo is first expelled, after the envelopes which surrounded it have been torn, and it is followed by the rest of the ovum. These envelopes are from without inwards—1. The *decidua reflexa* (p. 546). 2. The *chorion*, which, at the place where the allantois is situated (normally not at the orifice of exit of the uterus), forms the *placenta*, and which is free from villi over the *os uteri*. 3. The *amnion* (the umbilical vesicle forms an imperceptible structure in the placenta, compare p. 545).

As a result of the pressure of the first ‘pains,’ these membranes protrude in an arched form through the *os uteri*, and ultimately tear at one spot ; after a large part of the *liquor amnii* has escaped, a part of the foetus, usually the head, is set free. Now, with more or less rapidity, the process of expulsion sets in, hindered in part by the narrowness of the pelvis, in part by that of the *os uteri*, of the vagina and the vulva. Simultaneously, the placenta—not only its foetal, but also its maternal part, taking with it a portion of the uterine mucous membrane—detaches itself from the contracting uterine wall, a process which is naturally accompanied by hæmorrhage. After the birth of the foetus, the placenta, with the membranes which formed the walls of the ovum attached to its margins, though already detached, is still contained within the uterus, and the foetus is united to it by means of the long umbilical cord. The latter contains the following structures :—1. The stalk of the allantois (a prolongation of the urachus), with the umbilical vessels—viz., the two arteries, which continue to pulsate, and the vein, which by the early intra-uterine rotations of the foetus, is nearly always spirally twisted. 2. The shrivelled omphalo-meseraic duct with the umbilical vesicle. 3. Everything else which surrounds the tubular peduncle of the amnion projecting from the navel, and which thus covers the inner side of the placenta, and passes over its margin to those of

the chorion. The principal bulk of the umbilical cord is, however, formed by the three umbilical vessels, imbedded in a white connective tissue (*mucous tissue*), which is called 'Wharton's jelly.'

As soon as the detachment of the placenta commences, foetal respiration through the intermediation of the maternal blood ceases, and, in consequence of this, a change in the gases of the blood commences, which leads to the *first respiration through the lungs* (Schwartz). The placenta which is contained in the uterus is no longer of service to the child, and the umbilical cord, of which the arteries cease to pulsate, can, after previous ligature of its foetal end, be cut across, unless the expulsion of the placenta with the foetal envelopes ('*after-birth*') be awaited. The skin of the newly-born child is covered with a sebaceous layer, which constitutes the *vernix caseosa*. After the expulsion of the after-birth and the arrest of the hæmorrhage by the continuing contractions of the uterus ('*after-pains*'), a regeneration of the uterine mucous membrane sets in, which is accompanied by a diminution of its muscular coat, and a new formation of muscular fibre cells; the first of these processes is associated with a mucous, and at first bloody discharge, which constitutes '*the lochia*.'

At birth the mammary glands of the mother begin to secrete, and usually it is only on the cessation of the secretion, which takes place about ten months afterwards, that the process of menstruation, which had been arrested by impregnation, again becomes re-established.

D. DEVELOPMENT OF THE CHILD AFTER BIRTH.

At birth, neither the development of the structures nor of the functions of the young creature is arrested. The commencement of extra-uterine life, and the period which succeeds it up to *puberty*, are especially characterised by important processes of development. During this period (infancy and childhood) the development of the bones, and of the first and second teeth, takes place, and growth is most energetic; above all, it is the period of the development of the mental powers, which from the first low stages—when they approximate in their nature reflex actions, under the influence of the multiplicity of external influences, such as experience and education—develop ever more and more.

Growth is the term which is applied to express the increase in the dimensions of the body in all directions, as well as the increase of weight, due to the excess of the income of the body over its expenditure. The whole of the tissues and parts of the body take a part in this process, so that in general the *proportions* of the growing body are maintained. The most general concep-

tion of growth would treat it as being due to an *increase in the number* of tissue-forming elements, brought about in general as a result of cell-division, rather than as being due to an *increase in the size* of those which already exist, although this mode of growth also occurs.

The usual measure of its growth is the increase in the length of the body, and this is chiefly associated with the growth in length of the bones, which continues until about the twenty-second year. The growth in other dimensions, and the increase in weight, continues until about the fortieth year.

A diminution in *weight* occurs during the first days of life, and then again after from forty to fifty years of age; at the latter age this is associated with a diminution in the *length* of the body.

The life of man may be divided into the following periods: 1. 'Infancy,' which lasts from birth until the first dentition (the first 7 or 9 months); this is a period of most energetic growth, the length of the body increasing by two-thirds (20^{cm}). 2. 'Childhood,' which lasts until the second dentition (from 9 months until 7 years). The growth of the body in the second year amounts to about ten centimetres, in the third to about seven, and in each succeeding year about 5½^{cm}. 3. 'Boyhood and Girlhood,' which last until puberty (from 7 to 15 years). 4. 'Adolescence,' which extends to the completion of the growth of the body (15 to 22 years). 5. Period of maturity (adult age), which lasts until 'involution' occurs in woman, and until retrograde changes occur in man, i.e. from the twenty-second until the forty-fifth year. 6. Age of gradual retrograde changes (old age), commencing about the forty-fifth year and lasting until death.

The retrograde changes which occur in the later periods of life consist in manifold processes of wear and contraction and destruction, in which that which is diseased is so little separated from that which is healthy as to preclude any detailed allusion to the phenomena in this place.

E. DEATH.

Death puts an end to those processes of the organism which are characteristic of 'Life,' and with death there sets in an assemblage of processes which are comprehended in the term Putrefaction.

There may be great difference of opinion as to which is the act which marks the close of life. Most naturally the *energies* of the body, its movements and its heat production, especially the former, on account of their being easily recognised, appear to be conspicuous characteristics of life. It is obvious, however, that amongst movements, only one which is automatic can serve as an index of life, and of such automatic movements the most regular, as well as the most conspicuous, are those of the heart. Usually,

tion of growth would treat it as being due to an *increase in the number* of tissue-forming elements, brought about in general as a result of cell-division, rather than as being due to an *increase in the size* of those which already exist, although this mode of growth also occurs.

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A diminution in *weight* occurs during the first days of life, and then again after from forty to fifty years of age; at the latter age this is associated with a diminution in the *length* of the body.

The life of man may be divided into the following periods: 1. 'Infancy,' which lasts from birth until the first dentition (the first 7 or 9 months); this is a period of most energetic growth, the length of the body increasing by two-thirds (20^{cm}). 2. 'Childhood,' which lasts until the second dentition (from 9 months until 7 years). The growth of the body in the second year amounts to about ten centimetres, in the third to about seven, and in each succeeding year about 5^{cm}. 3. 'Boyhood and Girlhood,' which last until puberty (from 7 to 16 years). 4. 'Adolescence,' which extends to the completion of the growth of the body (16 to 22 years). 5. Period of maturity (adult age), which lasts until 'involution' occurs in woman, and until retrograde changes occur in man, i.e. from the twenty-second until the forty-fifth year. 6. Age of gradual retrograde changes (old age), commencing about the forty-fifth year and lasting until death.

The retrograde changes which occur in the later periods of life consist in manifold processes of wear and contraction and destruction, in which that which is diseased is so little separated from that which is healthy as to preclude any detailed allusion to the phenomena in this place.

E. DEATH.

Death puts an end to those processes of the organism which are characteristic of 'Life,' and with death there sets in an assemblage of processes which are comprehended in the term Putrefaction.

There may be great difference of opinion as to which is the act which marks the close of life. Most naturally the *energies* of the body, its movements and its heat production, especially the former, on account of their being easily recognised, appear to be conspicuous characteristics of life. It is obvious, however, that amongst movements, only one which is automatic can serve as an index of life, and of such automatic movements the most regular, and most conspicuous, are those of the heart. Usually,

then, the *standing-still of the heart* is looked upon as a sign of death.

Although it may be urged that the cessation of a single function cannot be taken as a sign of the cessation of all others, yet a continued cessation of the movements of the heart is a *certain* sign of *approaching* death, as the function of every organ is associated with a supply of arterialised blood, and this cannot be afforded without the heart. The standing-still of the heart is therefore one of the most certain causes of death.

The inquiry into the *causes of death* leads to the following conclusions. As the activities of the body are the result of oxidation processes, there are three forms of general (somatic) death, which may be due to—1. Deficiency in the material to be oxidised or of those inorganic matters which are indispensable to the vital processes, therefore *defective nutrition*. 2. Deficiency in the *supply of oxygenised blood*. 3. An absence of the *conditions necessary to the oxidising action* of oxygen.

Now, as these circumstances can exert their action upon one or all of the parts of the body, there may be either a general or only a local death. The latter (*necrosis, gangrene*) may, in its turn, lead to general death when it implicates an organ, the destruction of which is incompatible with life. The interlacement of the various processes of life renders it impossible to effect a strict separation between these three kinds of death; each of the three circumstances nearly always drags the others after it; it is therefore only necessary to examine these individually in so far as they furnish the *primary* causes of death.

I. *Defective nutrition* constitutes a very frequent, though always a remote cause of death (cessation of the action of the heart or respiratory muscles being the proximate cause). According to its nature it leads to a gradual death. Death from hunger, death which follows the inanition of old people, and also in part local death, due to local disturbances of the circulation, come under this category.

II. *The supply of arterialised blood* may be defective, or cease altogether—1. In consequence of the *absence of blood*, as when hæmorrhage occurs through the opening of large vessels, or of the heart itself. If the hæmorrhage be not fatal, a restoration may be brought about by the action of water, yet the amount of the red blood corpuscles may be so small as to be insufficient to keep up the necessary exchanges of oxygen. 2. By *cessation of the circulation*: this occurs (a) locally, by closure of the arteries going to a part (as by ligature, thrombosis, embolism, or by their being cut), or by a hindrance to the flow of blood, due to obstacles in the veins; the consequence may be local, or it may even be general death, if the disturbance of circulation affect the principal vascular trunks; (b) *generally, by a positive pressure in the*

thorax, or by an arrest of the heart; this may occur in consequence of injury or defective nutrition (atrophy) of the substance of the heart, of cessation of the circulation in the coronary arteries, of powerful irritation of the medulla oblongata or of the vagi, or of defective supply of oxygen. A cessation of the circulation is conceivable in consequence of the cardiac movements being completely *ineffective*—*e.g.* by an injury to, or inefficiency of the cardiac valves. 3. *By a hindrance to the absorption and retention of oxygen by the blood.* To this category belong all the influences mentioned at page 205, which lead to suffocation, of which some—viz. the cessation of the active movements of respiration—must now be examined more closely. The following circumstances lead to this—*a.* Paralysis of the respiratory centre in the medulla oblongata, due either to injury or destruction (*e.g.* by apoplexy); defective supply of blood or of oxygen due to circumstances which have already been mentioned; lastly, the action of paralysing poisons (such as chloroform). *b.* Impediments to the conducting power of nerves supplying the respiratory muscles, *e.g.* section or compression of the phrenic nerves and poisoning by curare. *c.* Paralysis of the respiratory muscles of the diaphragm. *d.* Tetanus of the respiratory muscles, as by strychnia-poisoning, or by irritation of the vagi. *e.* Mechanical hindrances to the expansion of the thorax, as pressure. 4. *By expulsion of the oxygen of the blood* (poisoning by carbonic oxide), or by a consumption of the oxygen of the blood (by means of reducing agents).

III. Very little is yet known concerning the circumstances required for the oxidation processes of the body. It has already been mentioned that the mean temperature of the body is indispensable to life. Great, or at any rate continuous, rises and depressions of the temperature (heating or cooling, with simultaneous abolition of the means of heat-regulation) lead to death. Possibly there are poisons which, like those which prevent putrefaction, render processes of oxidation impossible.

It belongs to the province of pathological science to investigate the modes in which diseases, injuries, and abnormal external circumstances, occasion death. Death from old age is usually designated as the physiological 'or natural' mode of death; this is a mode of death of which the proximate cause is unknown, but of which the remote causes are to be sought for in the diminished capacity for action of the organs of the body as a whole, and which is partly due to atrophy, partly to degeneration.

After the phenomena of 'rigor mortis' have passed away, the dead body falls a prey to putrefaction, unless this be prevented by very rapid desiccation or by the use of agents which oppose putrefaction. Putrefaction, concerning which little is yet known, consists in a slow oxidation of the organic consti-

tuents, brought about by the oxygen of the air, under the influence of a ferment such as vibrios must probably be considered (Pasteur).

The marks of post-mortem lividity (suggilations, livores) are precursors of putrefaction, which, in addition to cadaveric rigidity, afford an almost certain proof of death; these marks are occasioned by the blood-colouring matter diffusing out of the blood-corpuscles, first into the serum, and afterwards into the fluids moistening the arterial walls, the parenchyma of organs and the skin.

[APPENDIX TO CHAPTERS VIII. AND IX.]

THE time has now arrived when a more consecutive and organised account of the electrical phenomena of muscle and nerve is possible than that which is to be found in the body of this Text-book. It seems, therefore, desirable to supplement the account already presented to the student by a brief statement of the latest researches into the subject, and at the same time to help the student to put into their proper places the very numerous facts of which he has already become master. In order to do so, the editor of Hermann's 'Physiology' need not apologise for making use of the arrangement sanctioned by Professor Hermann himself, in a pamphlet containing a remarkably succinct historical and critical statement of the whole subject.

THE ELECTRO-MOTIVE PROPERTIES OF ORGANS AT REST.

Muscles of animals when in repose, and perfectly uninjured, never exhibit any differences of electric potential save such as are inseparable from all moist conductors. This is ascertained (1) by using only such muscle-preparations as have been made with scrupulous care, and especially such as have been defended from the extremely deleterious skin-secretion of the frog; (2) by using muscles which are still protected by their covering of skin, the currents proper to the latter having previously been destroyed by cauterizing the skin with salt-solution; (3) by testing the muscles of fishes through the skin, which is fortunately destitute of cutaneous currents; (4) by using the muscular tissue of the heart, which admits of ready preparation in an uninjured condition. In the course of this investigation it appears that cold did not, as was taught by Du Bois-Reymond, specially favour a currentless condition of the muscles.

But, in inflicting an injury upon a muscle, an electro-motive force can readily be demonstrated to exist, of such a nature that the injured portion has a negative electric potential in comparison with the uninjured portions. This electro-motive force must not be supposed to be pre-existent within the muscular tissue, for a certain interval of time is requisite for its development after the infliction of the injury: it is not a force which is merely unmasked, it is actually produced in the act of injury. This may be

demonstrated by means of a special apparatus, the Fall-Rheotome, for an exact description of which the English student is referred to Professor Burdon-Sanderson's 'Report' in 'Foster's Journal of Physiology.'¹

Not only does the protoplasmic tissue of muscle exhibit an electro-motive force where there is the contact of injured and dying portions with still living portions; other protoplasmic tissues, such as nerves, glands filled with uncoagulated blood, vegetable tissues, &c., under similar circumstances, exhibit similar currents. When they are injured by being cut with the knife, the cut surface assumes a lower electric potential than the rest of the organ, which is still normal.

That these currents are due to the contact of living and dying portions of tissue is clear from several considerations. Hermann himself observed that the cross sections of vegetable tissues assumed a very transitory negative potential, and that, when the negative potential had vanished, it could at once be restored by making a fresh section. This is readily explained on the assumption that dying tissue is necessary to the electro-motive force; for as soon as the death changes have destroyed the whole protoplasmic contents of the cells which are broken into by the knife in the act of section, the electro-motive conditions are removed. On the same assumption also it is easy to explain the observed fact that in certain long-fibred plants artificial longitudinal sections have a higher electric potential than artificial transverse sections; for the contents of the longitudinally split fibres die much more rapidly than the contents of the transversely divided ones. Of similar import are the recent observations of Engelmann on the currents caused by injuries to the muscular tissues of the heart, uterus, and intestines. Here the muscle-cells are small, and the death-changes are restricted to the cells which are actually injured during section, as in the case of the small-celled vegetable tissues mentioned above. And, in the last place, the similar transitional character of the currents of injury in nerves has been similarly explained by Engelmann; for in them the nodes of Ranvier, although permitting the passage of excitatory waves, yet confine the processes of death to the internode immediately injured by the knife.

The same proposition is still more ingeniously supported by Engelmann. If a living frog's muscle be subcutaneously divided, the negative potential of the artificial cross-section gradually diminishes and finally disappears, under the influences of the blood-circulation and of the nerves supplied to the part. The effect, therefore, of the restitutorial processes in muscle is to annul the

¹ A Report on Prof. L. Hermann's recent Researches on the Electro-motive properties of Muscle, by T. Burdon Sanderson. *Journal of Physiology*, vol. i. 196-212.

electro-motive force called forth by injuries. But if nature has so strong a tendency to counteract the electro-motive disturbance of artificial sections, it is probable that no muscle in a state of nature exhibits a current. Since the electro-motive force possessed by muscles which have suffered injury resides at the surface of contact of the living and dying tissue, Hermann proposes to call all such currents of injury, *boundary currents* (Demarcationsströme).

Not only are injuries to muscular tissue followed by the development of electro-motive forces, but a difference of temperature in the same muscular fibre has the same effect. Hermann has discovered that warm living portions of muscle have a higher electric potential than less warm living portions; and not only so, but that the same relation holds between warm living and cold dying tissue.

The conditions being known of the development of electro-motive force in individual muscular fibres, it is easy to understand the electrical phenomena of entire muscles. But as these, in their various forms of 'weak' and 'strong' currents, and 'currents of inclination,' are fully described in the body of the book, they will here be passed over.

ELECTROTONUS.

It was observed by Matteucci that, if the electrodes from a battery were applied to two points of a wire covered with some moistened conducting substance, certain currents could be demonstrated in the covered wire resembling the electrotonic currents of nerves already described (p. 349). If the wire were made of amalgamated zinc, and its sheath moistened with saturated solution of zinc sulphate, these currents ~~did~~ not appear, whence it was evident that they were due to polarization between the metallic cone and the moistening fluid of the sheath. Now nerves and muscles resemble the wire with its moistened covering in that they each consist of a peculiar tissue enclosed in a sheath of a different substance. Under the conditions of the above described experiment, therefore, they exhibit the same electrical phenomena, which are to be explained in the same manner as due to a polarization occurring between the sheath and its contents.

By the help of this doctrine of internal transverse polarization all the phenomena of electrotonus in nerve-trunks can be explained, and especially the circumstances that the electrotonic states require no appreciable time for their establishing; and that, when established, they cannot extend beyond a point of nerve that has been pinched through with a ligature.

The electrotonic phenomena of muscle are much more difficult to demonstrate than those of nerve.

ELECTRO-MOTIVE PROPERTIES DURING ACTIVITY.

A. *Muscle.*

Excitation travels along muscle and nerve in the form of a wave with a measurable rapidity. An examination of the electrical condition of such excited nerves and muscles discovers that there is associated with the excitatory wave in its course over the organ, a wave of negative potential which used to be called the 'wave of negative deflection.' In point of fact nervous or muscular tissue in the act of excitation exactly resembles dying tissue in its electrical relations to normal resting tissue. The currents caused by the contact of excited tissue with resting tissue are called by Hermann '*functional currents*' (Actionsströme). Of these there are two sorts, one associated with a single contraction (of muscle), the other associated with tetanus. When a single excitatory wave runs down a muscular fibre which is connected with a galvanometer at two spots, each spot will have a lower potential than the other as the excitatory wave passes it. Hence the functional current in the case of a single contraction consists of two distinct phases, of which the first, a descending current, may be termed '*atterminal*,' and the second, an ascending, '*abterminal*:' while the whole may be called the '*phasic functional current*.' The phases, when excised muscles are used, are never equally intense, the abterminal being invariably weaker than the atterminal. This difference is due to a diminution in the intensity of the excitatory wave in its course down the muscle, such as will be more fully described below.

What is here said applies both to the direct excitation of muscle and to excitation brought about through the nerves. In the latter case the excitatory wave starts from the mid-point of the muscular fibre, where the nerve enters, and travels thence towards both ends at once. At first the centre of the fibre is electrically negative in comparison with the ends; but afterwards the relation is reversed, and the ends acquire a negative potential. Thus each half of the fibre experiences the two successive phases, the '*atterminal*' and the '*abterminal*.' If the fibre presents an injured section, and if the excitatory wave is travelling towards the part injured, the second, abterminal, phase never appears, on account of the constant negative potential of the injured end.

If, on the other hand, the muscular fibre is tetanized—whether excitation travels in an undulatory form over the whole fibre or seize it as a whole—the electrodes must be the more negative the greater the excitatory value of the particular spot beneath them. The current obtained under these circumstances is called a '*tetanic*

functional current, and the nature of it will be better understood from a consideration of what follows.

In its progress along the fibres of an excised muscle, the excitatory wave experiences a diminution of intensity which is the more considerable as the muscle becomes more fatigued. Owing to this diminution of intensity, an excited spot near the starting point of the excitatory wave has a lower electric potential than an excited spot more remote. Hence, if a muscle be tetanized by stimuli applied to one end of it, and if the poles of a galvanometer be attached to two points of the tetanized muscle, one near and one remote from the point of stimulation, a current is obtained passing in the muscle from the stimulated towards the opposite extremity of the muscular fibres; and the magnitude of it is solely dependent upon the relative distances of the galvanometer electrodes from the stimulated spot. Such are the tetanic functional currents called forth by direct stimulation of muscles which are removed from the body but otherwise uninjured. When stimulated through their nerves, muscles exhibit the same phenomena. A functional current presents itself which is dependent upon the relative distances of the galvanometer poles from the '*nervous equator*' of the muscle, *i.e.* the equatorial plane in which the nerve-endings join the muscular fibres.

In the case of muscles possessed of an artificial cross-section, the tetanic functional current is somewhat masked. Assuming such a muscle to be tetanically stimulated at the end remote from the section, it is clear that the tetanic functional current will be opposed to the boundary current in direction, and will tend to counteract it. Hence the functional current will lead to a diminution or '*negative deflection*' of the boundary current; for which reason it has been called by Hermann a '*levelling*' or '*equalizing*' current (*ausgleichende*).

The diminution in intensity of excitatory waves as they pass along a muscle is only observed in the case of muscles removed from the circulation and not when they are under absolutely normal conditions. This may be strikingly demonstrated in the fore-arm of man. If one of the electrodes of a galvanometer circuit be applied to the skin of the fore-arm at the level of the '*nervous equator*'—about 10 cm. below the elbow—while the other is applied to the skin near the wrist, and if a single electric shock be given to the nerves of the brachial plexus through the skin of the arm, a phasic current may be demonstrated in the muscles of the fore-arm, the two phases of which are of equal intensity. For a similar reason it is impossible to arouse a tetanic functional current in the absolutely normal muscles of man, unless, perhaps, when they are greatly fatigued; for the rapid restitutional processes prevent the diminution of excitatory intensity upon which the tetanic functional current depends.

When an uninjured currentless muscle is thrown into activity by a stimulus affecting its whole mass at once, it never exhibits any functional current, whether the stimulus be single or tetanic; for in such a totally excited muscle the whole substance passes at the same moment into the same degree of excitation, and nowhere is the opportunity given for the contact of excited with non-excited or imperfectly-excited tissue. If the muscle possesses an artificial surface and a boundary current, the effect of total excitation is to cause a 'levelling' or 'equalizing' current which diminishes the current of injury.

It has long been known that a limb the muscles of which are voluntarily and violently contracted exhibits an ascending current which used to be ascribed (Du Bois-Reymond) to the algebraic summation of the tetanic functional currents of the contracted muscles. This explanation is now no longer tenable; and quite recently Hermann has observed that excitation of human muscles is followed by a secretory current in the superjacent skin which is directed from without inwards. This, doubtless, is the cause of the phenomenon.

B. *Nerve.*

A phasic functional current of uninjured nerves, though doubtless existing, has hitherto escaped detection, presumably owing to its exceedingly fleeting character; and there are theoretical reasons for believing that the tetanic functional current is self-destructive. For the excitatory undulations in nerve do not diminish in intensity in their course along the nerve, whence it is to be expected that the phases of the phasic current will turn out to be exactly equal. But, since the tetanic functional current is but the algebraic sum of a series of equal and opposite phases, it should always remain nil.

In nerves bounded by an artificial section and exhibiting a boundary current, the presence of functional currents has been detected both in the case of single and tetanic stimulation. In both cases it is a 'levelling' or 'equalizing' current, and brings about a diminution or negative deflection of the constant boundary current. The rate of transmission of the wave of negative deflection has been determined and found to be equal to the rate of conductivity of nerves deduced by other methods. This coincidence is taken as a proof of the identity of the processes in the two cases.

The most interesting effect of the functional currents of nerves is their effect upon the electrotonic currents. The electrotonic currents of a nerve, on excitation of the nerve, suffer diminution like the boundary current. This is due to the production of a functional current, owing to the polarized condition of the nerve,

which is opposite in direction to the polarizing and electrotonic currents. In order to explain this functional current it is assumed that the excitatory wave varies in intensity as it passes through the different electrotonic areas, becoming more intense as it approaches more positively or less negatively polarized portions of the nerve, and *vice versâ*. This is called the doctrine of the 'polarizational increment of excitation,' and it rests upon the following among other considerations. There is, during excitation of a polarized nerve, a powerful intrapolar current of like direction with the polarizer. This is not due to a diminution of the resistance offered by the nerve during the period of excitation, as was formerly supposed (Grünhagen), for the powers of resistance of nerves are in no wise altered during excitation (Hermann); but it is a distinct electro-motive phenomenon. It would follow directly from the above doctrine: since, according to it, the excitatory wave passing along the polarized nerve would be most intense at the polarizing anode and least intense at the polarizing cathode—precisely the electro-motive conditions which are favourable for the production of such an intrapolar current.]

[The advanced student who may wish to consult the original memoirs which form the basis of the above account, is referred to the following list:—

- Die Ergebnisse neuerer Untersuchungen auf dem Gebiete der thierischen Electricität. L. Hermann, 1868.
- Untersuchungen über die Entwicklung des Muskelstroms. Pflüg. Arch. vol. xv. p. 191.
- Versuche mit dem Fall-Rheotom über die Erregungsschwankung des Muskels. Pflüg. Arch. vol. xv. p. 233.
- Untersuchungen über die Actionsströme des Muskels. Pflüg. Arch. vol. xvi. p. 191.
- Ueber den Actionsstrom der Muskeln in lebenden Menschen. Pflüg. Arch. vol. xvi. p. 410.]

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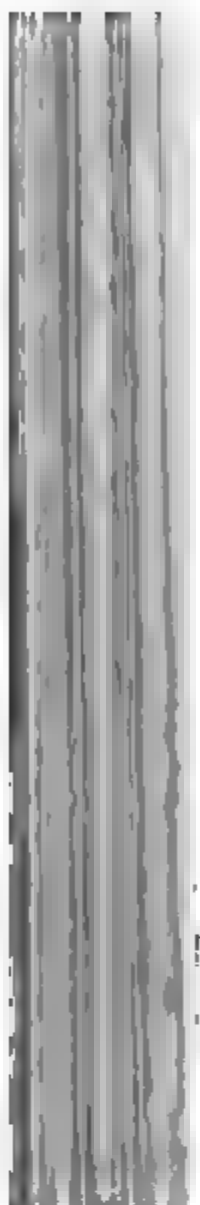
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